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Dimorphic spermatozoa of the hydrothermal vent prosobranch *Alviniconcha hessleri* : systematic importance and comparison with other caenogastropods

by John Healy

Abstract. — Ultrastructural features of euspermatozoa and paraspermatozoa of *Alviniconcha hessleri* Okutani & Ohta are described and compared with available data for other gastropods. Euspermatozoa are filiform, 130-135 μm long, with a conical acrosomal vesicle (featuring an apical bleb), a curved, rod-shaped nucleus, an elongate midpiece (with 10-11 helically coiled mitochondrial elements), an annular complex, a glycogen piece and an end piece. An unusual sheath of dense material of uncertain origin is associated with the nucleus and the midpiece. Apart from this sheath, most other features of *Alviniconcha* euspermatozoa occur in euspermatozoa of the Neotaenioglossa (in particular groups such as the Loxonematoidea (Abyssochrysidae), Vermetoidea, Calyptraeoidea, Littorinoidea, Truncatelloidea) and certain Neogastropoda. Paraspermatozoa of *Alviniconcha* consist of large, moderately electron-dense vesicles, smaller, highly electron-dense bodies and occasional mitochondria all enclosed by the plasma membrane. These cells lack axonemes, recognizable nuclear material and an acrosome. Although similar 'nurse cell' type paraspermatozoa associate with euspermatozoa to form spermatozeugmata in the Littorinoidea and Abyssochrysidae, this phenomenon was not observed in *Alviniconcha*. Sperm ultrastructure indicates that *Alviniconcha* belongs within the Neotaenioglossa and is more closely allied to the Littorinoidea-Loxonematoidea than to the Calyptraeoidea or Hipponicoidea. Specifically, sperm data do not support a close relationship between *Alviniconcha* and the Architaenioglossa, the Cerithioidea or the Trichotropidae, but are consistent with a recent proposal to include the genus within the loxonematoidean family Provannidae.

Résumé. — Les caractéristiques ultrastructurales des euspermatozoïdes et paraspermatozoïdes d'*Alviniconcha hessleri* Okutani & Ohta sont décrites et comparées à celles d'autres gastéropodes. Les euspermatozoïdes sont filiformes, et mesurent 130 à 135 μm de long; ils ont une vésicule acrosomiale conique (avec bulle apicale), un noyau en forme de bâtonnet recourbé, une pièce intermédiaire allongée (avec 10-11 éléments mitochondriaux enroulés en hélice), un complexe annulaire, une pièce à glycogène et une pièce terminale. On observe également un manchon inhabituel de matériel dense, d'origine inconnue, associé au noyau et à la pièce intermédiaire. A l'exception de ce manchon, la plupart des caractéristiques des euspermatozoïdes d'*Alviniconcha* se rencontrent également chez les euspermatozoïdes des Neotaenioglossa — en particulier des groupes comme les Loxonematoidea (Abyssochrysidae), Vermetoidea, Calyptraeoidea, Littorinoidea, Truncatelloidea — et des Neogastropoda. Les paraspermatozoïdes d'*Alviniconcha* consistent en un ensemble de grandes vésicules, modérément denses aux électrons, des corps plus petits, très denses aux électrons, et quelques mitochondries, le tout enfermé par la membrane plasmique. Ces cellules n'ont ni axonème, ni matériel nucléaire reconnaissable, ni acrosome. Chez les Littorinoidea et les Abyssochrysidae, de tels paraspermatozoïdes de type « cellules nourricières » s'associent aux euspermatozoïdes pour former des spermatozeugmata : un tel phénomène n'a pas été observé chez *Alviniconcha*. L'ultrastructure des spermatozoïdes montre qu'*Alviniconcha* appartient aux Neotaenioglossa et qu'il est plus proche de la lignée Littorinoidea-Loxonematoidea que des Calyptraeoidea ou des Hipponicoidea. Dans tous les cas, ces données démentent l'idée d'une relation proche entre *Alviniconcha* et les Architaenioglossa, les Cerithioidea ou les Trichotropidae, mais appuient au contraire la proposition récente de classer ce genre dans la famille Provannidae (Loxonematoidea).

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Introduction

Exploration of deep sea hydrothermal vents continues to reveal an interesting and taxonomically significant array of prosobranch gastropods (Fretter, 1988; Lutz *et al.*, 1986; McLean, 1981, 1988*a-c*, 1989; Warén & Bouchet, 1986, 1989). Although the majority of these species are 'archaeogastropods' *sensu lato* (for example see Hickman, 1984; McLean & Haszprunar, 1987; McLean 1988*a-b*, 1989) a number of unusual caenogastropods have also emerged from the vent communities (Warén & Bouchet, 1986; Warén & Ponder, 1991; Bouchet & Warén, 1991). In describing *Alviniconcha hessleri* from vents in the Mariana Back-Arc Basin, Okutani & Ohta (1988) expressed uncertainty as to the true systematic position of their new species and genus. Shell features and the presence of well developed periostracal hairs suggested affinities with the Trichotropidae (Calyptraeoidea), while radular shape and formula indicated a possible connection with the Hipponicoidea (see Okutani & Ohta, 1988). Most recently Bouchet & Warén (1991) have placed *Alviniconcha* and *Ifremeria* into the Provannidae, a family established by Warén & Ponder (1991) for another hydrothermal vent genus *Provanna*. Warén & Ponder (1991) tentatively assigned the Provannidae to the Loxonematoidea to join another family of this relict group, the Abyssochrysidae (see Houbrick, 1979). On the basis of comparative anatomy Bouchet & Warén (1991) concluded that any shell similarities between the Provannidae and the Viviparidae or Trichotropidae were of a superficial nature only. Beck (1991) has, in contrast, suggested that *Olgaconcha* (a synonym of *Ifremeria* Bouchet & Warén, 1991 [1]) and *Alviniconcha* may be closely related to the Architaenioglossa (eg Viviparidae) or the Cerithioidea.

Previous studies have shown that sperm morphology in the Mollusca reflects not only the environment of fertilization (eg Franzén, 1955) but also the systematic position of taxa from the level of species upwards (Popham, 1979; Kohnert & Storch, 1984; Healy, 1982, 1983*a*, 1986*a, b*, 1988*a, b*, 1990*a-c*; Koike, 1985; Hodgson & Bernard. 1988; Hodgson *et al.*, 1988). In particular, within the prosobranch order Caenogastropoda (= Mesogastropoda + Neogastropoda), a reasonably good data base now exists with which to test views on the likely position of newly discovered taxa such as *Alviniconcha*.

During the course of the present study it became obvious that sperm ultrastructural data for the Trichotropidae would be needed for comparison with *Alviniconcha*. I have therefore included herein a brief description and salient micrographs of the euspermatozoa and paraspermatozoa of a representative trichotropid, *Trichosirius inornatus* (Suter) from New Zealand. It is hoped that this study may stimulate further ultrastructural work on sperm morphology of hydrothermal vent molluscs.

Materials and methods

Live *Alviniconcha hessleri* Okutani & Ohta, 1988 were collected during the BIOLAU cruise of the Lau Basin, south-east of Fiji, using the submersible craft 'Nautile' (12-27 May,

1. Dr. P. Bouchet advises (in litt.) that *Olgaconcha tufari* Beck, 1991 is a synonym of *Ifremeria nautilei* Bouchet & Warén, 1991. The paper by Bouchet & Warén (1991) was published before that of Beck (1991), hence the name *Ifremeria nautilei* Bouchet & Warén must take priority over *Olgoconcha tufari* Beck.

1989). Collection data for this material are as follows : dive 12 on site Vailili, Valufa Ridge, Lau Basin, 23°13′ S, 176°38′ W at a depth of 1,750 m (Observer for this dive was P. CRASSOUS, IFREMER, Brest). The material examined herein consists of sperm-filled, sac-like outpockets of the distal end of the sperm duct (as described by WARÉN & BOUCHET, 1992). Voucher specimens of *Alviniconcha hessleri* have been deposited in the Muséum national d'Histoire naturelle (Paris). Tissues were fixed in cold (0-4° C) cacodylate-buffered glutaraldehyde then dispatched to the author for subsequent processing and analysis. Small pieces of the sperm sacs were taken from the samples provided and processed for transmission electron microscopy (TEM) according to the following schedule : (1) rinse in cold 0.1 M cacodylate buffer containing 10 % sucrose (1 hr); (2) osmication of tissues for two hours (1 % osmium tetroxide in cacodylate or phosphate buffer); (3) buffer rinse; (4) gradual dehydration using ethanol; (5) embedding in Spurr's epoxy resin. For comparison with *Alviniconcha hessleri*, portions of the sperm duct of a representative trichotropid, *Trichosirius inornatus* (Suter), were processed for TEM. This material derives from sea water formalin-fixed specimens collected by W. F. PONDER (June 1966). After rinsing in phosphate buffer, tissue pieces of *Trichosirius inornatus* were processed as outlined above for *Alviniconcha hessleri*. All ultrathin and semithin sections were prepared with an LKB IV Ultrotome. Ultrathin sections were stained using DADDOW's (1986) modified double lead procedure and examined with a Hitachi 300 TEM operated at 75kV. Tissue squashes were also examined by standard phase-contrast as well as Nomarski-phase contrast light microscopy using an Olympus BH2 light microscope.

RESULTS

EUSPERMATOZOA

Euspermatozoa of *Alviniconcha hessleri* (hereafter referred to as *Alviniconcha*) are filiform, approximately 130-135 μm long and comprise an acrosomal complex, nucleus, midpiece, annular complex, glycogen piece and end piece.

Acrosomal complex : The acrosomal vesicle is conical, 0.9 μm long and posteriorly circular in transverse profile (pl. I C-F). It rests on a thin, basal plate which is grooved to fit the nuclear apex (pl. I E, F). An accessory membrane attached to the basal plate sheaths the posterior 0.5 μm of the acrosomal vesicle (pl. I D-F). Anteriorly the vesicle membrane expands away from the vesicle contents to form an electron lucent space : the apical bleb (pl. I B, E, F). Oblique transverse sections reveal the presence of radially arranged plates within the matrix of the acrosomal vesicle (pl. I D). A basal invagination, extending almost to the apex of the vesicle, contains subacrosomal material organized as an axial rod embedded in a granular matrix (pl. I C-F).

Nucleus : TEM confirms light microscopic observations that the euspermatozoan nucleus of *Alviniconcha* is slightly curved (pl. I A). The nucleus is cylindrical (diameter 0.4 μm posteriorly, tapering to 0.2 μm anteriorly) and approximately 7.5 μm long, with narrow basal invagination (0.76 μm deep) which forms the attachment site for the centriolar derivative and axoneme (pl. I A, G, H; II A, E). An extensive, irregularly shaped sheath of finely granular

material is associated with the surface of the nucleus, particularly in the middle to basal regions where nuclear contents sometimes appear fibrous in substructure (pl. I G-J ; II A). Although 'ballooning' of the plasma membrane away from the surface of the nucleus (pl. I A, I, pl. II A) could prove to be an artifact of fixation, the localization of this phenomenon, and the generally good preservation of other cell components tend to argue against this. As plate I and plate II show, the dense sheath penetrates into the anterior region of the midpiece where it partially surrounds the axoneme, and frequently the mitochondrial elements themselves. The absence of developing euspermatozoa prevents any resolution of the origin or purpose of the sheath substance. The varied shape and thickness of the sheath suggests either that this structure is genuinely variable in its morphology or that it may not have reached its final form (i.e. the observed euspermatozoa are still in the process of maturation).

Midpiece : The midpiece exhibits ten to eleven mitochondrial elements which wind helically around a 9 + 2 pattern anoxeme (pl. I G, H, K ; II C-F). Each element has flattened adjoining surfaces and contains scattered, poorly developed cristae (pl. II C-F). As previously mentioned the dense sheath observed in the nuclear region also occurs within the midpiece and the nucleus-midpiece junction (pl. I G, H, K ; II E, D). Longitudinal sections through the anterior portion of the midpiece show that the sheath surrounding the midpiece elements or the axoneme is often discontinuous suggesting segmentation (pl. I G, H ; II D). In some euspermatozoa, sheath material associated with the axoneme appeared to be helically arranged (see pl. II F). The midpiece measures between 76 and 80 μm in length (light microscopic observations).

Annular complex, glycogen piece, end piece : The annular complex occurs at the junction of midpiece and glycogen piece. It comprises a dense ring or 'annulus' (applied to the inner surface of the plasma membrane) and a closely associated collar of dense material which lines the terminal 0.4 μm of the mitochondrial membrane (pl. III A). Within the glycogen piece each of the nine axonemal doublets is associated with a tract of dense, putative glycogen granules (pl. III A, B). As plate III C shows, the glycogen piece ends abruptly, leaving the end piece of the euspermatozoon to consist solely of the plasma membrane and axoneme. The combined length of the glycogen piece and end piece varies from 46 to 50 μm (light microscopic observations).

Paraspermatozoa

Paraspermatozoa of *Alviniconcha hessleri* are rounded cells containing the following features : (1) a variable number (5-8) of large, membrane-bound, spherical vesicles ; (2) one to three spherical, highly electron dense bodies, (3) a finely granular, background matrix (4) a delimiting, plasma membrane (pl. III D, E). Mitochondria were only rarely observed. No evidence of an acrosome, axonemes (either contained within the parasperm body or emergent as tails) or centrioles could be found. In spite of the absence of developing paraspermatozoa in material studied, comparison with other caenogastropods suggests that the larger vesicles are probably products of Golgi and/or endoplasmic reticular activity. The origin of the smaller, more highly electron-dense bodies (pl. III D, E) is more difficult to determine. There remains the possibility that these bodies are condensed nuclear remnants (caryomerites' of authors) but

the absence of a double nuclear membrane around the bodies or any evidence of fibrillar/coarse granular substructure or lacunae argue against this view. Wherever the large vesicles touch, their surfaces are flattened (pl. III D). Undoubtedly this affords efficient packing of vesicles and a certain degree of structural integrity for the paraspermatozoon as a whole. Paraspermatozoa and euspermatozoa of *Alviniconcha hessleri* were never observed in contact with each other, suggesting that spermatozeugmata are probably not formed in this species.

Trichotropidae
(*Trichosirius inornata* Suter)

Euspermatozoa

Acrosomal complex : The acrosomal vesicle is conical and deeply invaginated with a prominent apical bleb (pl. IV A). It has a maximum diameter of 0.3 μm near the base, and average length of 1.0 μm. Apically the vesicle is sometimes curved or slightly hooked, suggesting that this organelle is flexible. A rod-shaped deposit of subacrosomal material runs almost the full length of the vesicle invagination (0.67-0.7 μm). A thin, centrally perforate, basal plate lies between the basal rim of the acrosomal vesicle and the nuclear apex. Although longitudinal sections suggest the presence of an accessory membrane, the precise extent of this feature could not be determined.

Nucleus : The euspermatozoon nucleus is elongate (approximately 50-54 μm long, light microscopic observations), tubular and encloses the centriolar derivative and anterior portion of the axoneme (pl. IV A-C, F). Nuclear contents are highly electron dense and decrease in extent anteriorly until only a thin layer (0.02 μm thick) surrounds the centriolar derivative (pl. IV A, C, F). Nine microtubular elements embedded in dense material constitute the centriolar derivative, however the exact substructure of these elements was not determined. The axoneme appears to show the typical 9 + 2 configuration. Diameter of the nucleus, including the nuclear and plasma membranes and enclosed axoneme decreases from 0.56 μm posteriorly to 0.33 μm near the acrosome.

Midpiece : The midpiece begins immediately posterior to the nucleus and comprises the axoneme (continuing from the nuclear region) surrounded by five to six helically coiled, mitochondrial elements (pl. IV B, D, E, G). Each of the mitochondrial elements exhibits random, unmodified cristae (pl. IV D, E). The midpiece measures approximately 12 μm (light microscopic observations).

Annular complex, glycogen piece : Longitudinal or oblique longitudinal sections revealed that an annular complex is present at the junction of the midpiece and glycogen piece. This complex consists of two distinct rings, each connected to the inner surface of the plasma membrane and each showing a triangular profile in longitudinal section (pl. IV E). The glycogen piece is recognized by the nine spoke-like structures connecting the doublets with the plasma membrane (pl. IV G). Although transverse sections were obtained showing evidence of periaxonemal granules attached to the spokes most euspermatozoa seemed to lack such

deposits. This is almost certainly due to the fixation deficiencies of the formalin preserved material available for study. The numerous individual axonemes observed (all associated with disrupted plasma membranes) are here interpreted as the terminal or end piece of the euspermatozoon. Light microscopy gives a length of 12 μm for the glycogen piece and end piece combined.

Paraspermatozoa

Paraspermatozoa of *Trichosirius inornatus* are vermiform cells, 24 to 32 μm long (light microscopic observations) which are composed of longitudinally aligned axonemes, scattered mitochondria, numerous oblong, dense vesicles and a granular cytoplasm (pl. IV F, G). Transverse sections show that mature cells are laterally compressed, but moreso anteriorly where mitochondria are positioned between the axnemes (pl. IV F). All parasperm organelles are contained within a common plasma membrane. Axonemes are positioned peripherally, close to or in contact with the inside surface of the plasma membrane. Towards the posterior region of the cell, the axonemes project into shallow outpockets of the plasma membrane (pl. IV F, G). No evidence of physical contact between paraspermatozoa and euspermatozoa (eg spermatozeugmata formation) was observed in *Trichosirius inornatus*.

DISCUSSION

Structural comparison

The presence of paraspermatozoa and more importantly the morphology of the euspermatozoa clearly identifies *Alviniconcha* as a caenogastropod. Caenogastropods can be divided into two main groups on the basis of euspermatozoan features, notably the substructure of the acrosome and midpiece (Healy, 1988*a*). These groups are : (1) the Cerithioidea, Ampullarioidea and Cyclophoroidea and (2) the remainder of the Caenogastropoda. The first of these groups is characterized by absence of an apical bleb and accessory membrane in the acrosomal complex and presence of highly organized, parallel cristal plates in the mitochondrial elements. *Alviniconcha* belongs to the second, larger group of caenogastropods, the euspermatozoa of which possess an apical bleb (sometimes poorly developed), an accessory membrane (also present in the enigmatic bridging group Campaniloidea — see Healy, 1986*b*), and 5 to 11 helically coiled mitochondrial elements (cristae usually unmodified, sometimes tubular). In all caenogastropod euspermatozoa with the exception of the truncatelloidean *Stenothyra* sp. (Healy, 1983*b*), the glycogen piece exhibits nine periaxonemal tracts of granules. Elsewhere within the Mollusca this arrangement of sperm glycogen deposits occurs in the Octopoda (Longo & Anderson, 1970).

Euspermatozoa of *Alviniconcha* differ from those of other caenogastropods in possessing a well developed sheath of electron dense material which extends from the nucleus into the anterior portion of the midpiece. An absence of spermiogenic stages in material available for

study prevented any determination of the origin of this dense sheath. The frequently observed 'disjointed' nature of the sheath within the *Alviniconcha* midpiece invites comparison with the segmented midpiece sheath observed in euspermatozoa of the relict campaniloidean *Campanile symbolicum* Iredale (see HEALY, 1986*b*). Although the origin of the *Campanile* sheath is also unknown, it is, in contrast to the *Alviniconcha* sheath, composed of equal-sized elements which are membrane bound and never associated with the nucleus. In *Alviniconcha* the dense sheath is well developed in the region of the nucleus (actually contacting the nuclear surface), while posteriorly, it often extends around the axoneme and midpiece elements. Spermatozoa of certain stylommatophoran pulmonates also possess a non-membrane bound perinuclear sheath which may be layered (eg *Helix aspersa* (Müller); HEALY & JAMIESON, 1989) or exhibit paracrystalline substructure (eg *Oxyloma elegans* (Risso); SELMI *et al.*, 1989). In *Oxyloma elegans*, the sheath disappears during storage in the seminal receptacle (SELMI *et al.*, 1989). Unlike *Alviniconcha*, the sheath in pulmonate sperm does not also extend into the midpiece. The marked variation in thickness and distribution of the dense sheath in *Alviniconcha* suggests that this structure perhaps has not attained its final form (? a late spermiogenic feature) or alternatively, is genuinely variable in its morphology. Detailed study of spermatids and seminal receptacle spermatozoa will help determine the origin and possible function of the sheath material. Even if the observed sheath is not fully mature in its form or proves to be a transient feature, its presence distinguishes *Alviniconcha* from other caenogastropods. I will return to the possible taxonomic implications of *Alviniconcha* eusperm morphology in the final section of this discussion.

Paraspermatozoa of *Alviniconcha* closely resemble those of the Littorinoidea (especially *Littorina*, see BUCKLAND-NICKS & CHIA, 1977) and the loxonematoidean *Abyssochrysos brasilianum* Bouchet (see HEALY, 1990*a*). In paraspermatozoa of all three taxa, an acrosome, axonemes and centrioles are absent, and large secretory vesicles suspended within a granular matrix constitute the bulk of the spherical cell body. In *Abyssochrysos*, the littorinid subfamily Littorininae and the atlantoidean *Carinaria lamarcki* Péron & Lesueur, euspermatozoa attach in an organized cluster to each paraspermatozoon to form spermatozeugmata (REINKE, 1912; BUCKLAND-NICKS & CHIA, 1977; THIRIOT-QUIEVREUX & MARTOJA, 1979; KOHNERT & STORCH, 1984; REID, 1986; HEALY, 1990*a*). Spermatozeugmata were not observed in *Alviniconcha* but this is also the case in certain littorinids which possess 'nurse cell' type paraspermatozoa such as the genus *Peasiella* (REID, 1989) and probably the genus *Provanna* (Provannidae, Loxonematoidea — see WARÉN & PONDER, 1991). Although the large vesicles of *Alviniconcha* paraspermatozoa are probably products of Golgi and/or endoplasmic reticular activity (as occurs in other caenogastropods), the likely origin of the highly electron-dense bodies is problematical. Two alternatives seem possible. Either these bodies represent condensed nuclear remnants (= 'caryomerites') or they are another form of secretory product. Observations on parasperm development would help to clarify this issue, but for the present it is worth noting that the dense bodies are enclosed by a single and not a double (eg nuclear) membrane and that the bodies show no evidence of nuclear substructure such as fibrils, coarse granules or lacunae. Although paraspermatozoa of most littorinids and *Abyssochrysos* do not retain a nuclear fragment (BUCKLAND-NICKS & CHIA, 1977; REID, 1986; HEALY, 1990*a*) some species do (REID, 1986). Retention of condensed nuclear material in caenogastropod paraspermatozoa is not unusual for certain taxa (eg Cyclophoroidea, Cerithioidea; SELMI & GIUSTI, 1980; HEALY, 1986*a*, 1988*a*).

Systematic implications

The systematic position of *Alviniconcha* was briefly discussed by Okutani & Ohta (1988) in their account of the new species and genus. They suggested a possible link between *Alviniconcha* and the calyptraeoidean family Trichotropidae (conchological features including prominent 'hairy' periostracum) or, in view of radular features perhaps a closer connection between the genus and the Hipponicoidea [1]. Beck (1991) believes that *Alviniconcha* and *Olgaconcha* (a synonym of *Ifremeria* Bouchet & Warén, 1991; see footnot 1, p. 274) may be closely related to the Architaenioglossa (Vivipariidae and allies) or the Cerithioidea. A stronger case, favouring loxonematoidean affinities for *Alviniconcha* has been put forward by Warén & Bouchet (1992).

Comparative sperm data for the Caenogastropoda, despite being fragmentary for the Calyptraeoidea and Hipponicoidea, provide some basis for evaluating these differing views concerning the relationships and systematic position of *Alviniconcha*. To begin with, let us consider the possibility of a Calyptraeoidea or Hipponicoidea connection. Some genera of the Calyptraeoidea (for example *Calyptraea, Crepidula*) possess a short eusperm nucleus (Kohnert & Storch, 1984) like *Alviniconcha*, while in other genera such as *Trichosirius* (this study) and the Hipponicoidea (*Vanikoro*; Healy, 1984) it is long and tubular. The value of eusperm nuclear shape in the Caenogastropoda is limited, for in some families (eg Littorinidae, Turridae, Eulimidae, Terebridae) different genera may show short *or* tubular nuclei (although the shape appears consistent in any given genus) (Healy, 1984, 1988*a*; Kohnert & Storch, 1984; Koike, 1985). Other euspermatozoan features such as the acrosomal complex, midpiece and glycogen piece of *Alviniconcha* are similar to those seen in the Calyptraeoidea, Hipponicioidea and in fact many other caenogastropod superfamilies (Bulnheim, 1962; Healy, 1984, 1988*a, b*, 1990*b*; Kohnert & Storch, 1984; Koike, 1985). The dense sheath of *Alviniconcha* euspermatozoa is not, however, seen in any other group (the segmented sheath of *Campanile* being here regarded as non-homologous). More significantly perhaps than eusperm morphology, the paraspermatozoa of the Calyptraeoidea (*Crepidula*, Gould, 1917; *Trichosirius*, this study) are vermiform cells with multiple, internal axonemes and small secretory vesicles. This type of paraspermatozoon, also recorded in other caenogastropod groups such as the Cypraeoidea, Dolioidea, Muricoidea (Melone *et al.*, 1980; Healy, 1988*a*), contrasts with the round paraspermatozoa of *Alviniconcha* which exhibit large secretory vesicles lack axonemes. No data on the presence or structure of paraspermatozoa in the Hipponicoidea or the Fossaridae are at present available, the latter family being transferred to the Cerithioidea (now as subfamily of Planaxidae; see footnote 1, p. 274). To sum up, eusperm and parasperm structure do not provide any overwhelming support for a connection between *Alviniconcha* and the Calyptraeoidea or the Hipponicoidea (specifically the Trichotropidae).

A large body of information now exists on the fine structure of euspermatozoa and paraspermatozoa in the Architaenioglossa (Ampullarioidea, Cyclophoroidea) and the Ceri-

1. In their discussion of the relationships of *Alviniconcha*, Okutani & Ohta (1988) cite the Fossaridae as a member family of the Hipponicoidea. Anatomical studies have shown that species of the genus *Fossarus* share a cephalic brood pouch with the Planaxidae, and partly on this basis the Fossaridae were transferred to the Cerithioidea (Ponder, 1980; Ponder & Warén, 1988). Houbrick (1990) has subsequently reduced the Fossaridae to the status of subfamily within the Planaxidae.

thioidea (for principal references see HEALY, 1983*a*, 1986*a*, 1988*a*; KOHNERT & STORCH, 1984; KOIKE, 1985). These groups are united by many similarities in eusperm and parasperm morphology, but do not share any significant similarities with either the euspermatozoa or paraspermatozoa of *Alviniconcha*. On this basis I cannot support BECK's (1991) suggestion that *Alviniconcha* or *Olgaconcha* (= *Ifremeria*) may be closely related to the Architaenioglossa or the Cerithioidea.

A further view, that of an *Alviniconcha*-Loxonematoidea relationship (proposed by BOUCHET & WARÉN, 1991) seems much more promising than those already considered above, primarily because the only caenogastropod known to possess similar euspermatozoa *and* paraspermatozoa to *Alviniconcha* is *Abyssochrysos brasilianum* Bouchet (Abyssochrysidae, Loxonematoidea). There are a few differences however. Unlike *Alviniconcha*, euspermatozoa and paraspermatozoa of *Abyssochrysos* definitely form spermatozeugmata similar to those of many Littorinidae (HEALY, 1990*a*; see also BUCKLAND-NICKS & CHIA, 1977). Secondly, the dense sheath of *Alviniconcha* euspermatozoa is lacking in *Abyssochrysos*. Absence of spermatozeugmata in *Alviniconcha* may not be as taxonomically significant as it first appears because the same situation has been noted in *Provanna* (recently transferred to Loxonematoidea) and in certain littorinids (REID, 1989; WARÉN & PONDER, 1991). Eusperm nuclei of *Provanna* differ from those of *Alviniconcha* in being elongate and tubular rather than short and solid (HEALY, 1990*c*).

In conclusion, sperm morphology supports a close relationship between deep-sea taxa such as *Alviniconcha, Abyssochrysos* and *Provanna*, and other basal neotaenioglossans notably the Littorinoidea. BOUCHET & WARÉN (1991) have grouped *Provanna, Alviniconcha* and *Ifremeria* within the Provannidae (of WARÉN & PONDER, 1991), and following WARÉN & PONDER, tentatively included this family in the Loxonematoidea (to join the Abyssochrysidae). In spite of anatomical differences, the Littorinoidea and Loxonematoidea (now including Abyssochrysidae and Provannidae) significantly exhibit the same eusperm and parasperm morphology. This similarity may prove to be due to symplesiomorphy, although it is by no means certain that the 'nurse cell' paraspermatozoon of the Littorinoidea and Loxonematoidea is in fact a basal, unspecialized type relative to the axonemal paraspermatozoa of other caenogastropods (see JAMIESON, 1987 for further discussion). In other lower neotaenioglossan superfamilies, paraspermatozoa appear to be absent in the Truncatelloidea and Cingulopsoidea (HEALY, 1984; but see PONDER, 1983 for the possibility of parasperm in Barleeidae) while euspermatozoa and paraspermatozoa of the Cerithioidea and Architaenioglossa show numerous differences from those of the Littorinoidea and Loxonematiodea (see HEALY, 1983*a*, 1986*a*, 1988*a* for comparison and further references). Undoubtedly as knowledge of sperm structure in basal groups within the Neotaenioglossa improves, a clearer picture of the phylogeny of this caenogastropod assemblage will emerge.

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PLATE I

Alviniconcha : euspermatozoa

A — Longitudinal section (L.S.) through acrosome, nucleus and proximal portion of midpiece. Note expanded plasma and nuclear membranes (*).

B-C — Series of transverse sections (T.S.) from apex to base of acrosomal complex. Plate substructure visible in wall of vesicle in pl. I D (arrow heads).

D, E — L.S. acrosomal complex and nuclear apex of two euspermatozoa.

G, H — L.S. junction of nuclear invagination and proximal portion of midpiece. Note disjointed nature of dense sheath associated with axoneme and mitochondrial elements.

I, J — T.S. nuclei and dense sheath.

K — T.S. junction of nucleus and midpiece.

Scale bars : A = 1.0 μm; G, H = 0.5 μm; B-F, K, J = 0.25 μm

Abbreviations used in the figures : a, acrosomal complex; ab, apical bleb; am, accessory membrane (of acrosomal complex); an, annular complex; ar, axial rod (of acrosomal complex); av, acrosomal vesicle; ax, axoneme; bp, basal plate (of acrosomal complex); c, centriolar derivative; ds, dense sheath (of euspermatozoon); ep, end piece; eu, euspermatozoa; gp, glycogen piece; m, unmodified mitochondrion; M, midpiece; mpe, midpiece (mitochondrial) elements; n, nucleus; p, paraspermatozoon; pm, plasma membrane; v, oblong vesicles.

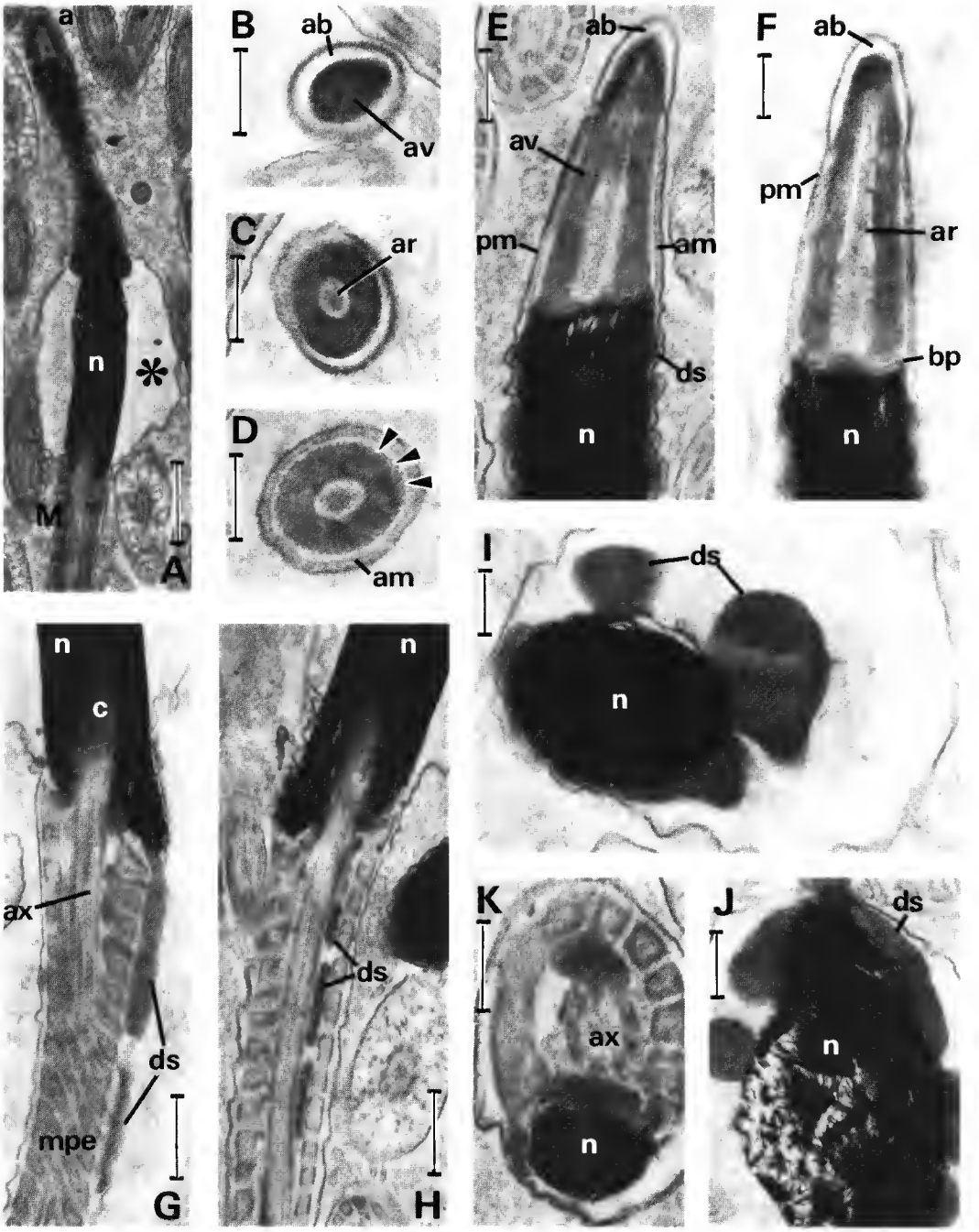
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PLATE I

PLATE II

Alviniconcha : euspermatozoa

A — L.S. base of nucleus showing expanded nature of plasma and nuclear membranes (*).
B — T.S. nucleus and dense sheath.
C — T.S. midpiece. Note dense sheath associated with periaxonemal surface of mitochondrial elements.
D — L.S. proximal portion of midpiece showing dense sheath associated with mitochondrial elements and axoneme. Inset : T.S. same region of midpiece.
E — L.S. junction of nucleus and midpiece showing seemingly 'fluid' nature of dense sheath.
F — L.S. midpiece showing slight spiralling of dense sheath around axoneme. Inset : same region of midpiece.

Scale bars : A = 0.5 μm; B-F = 0.25 μm.

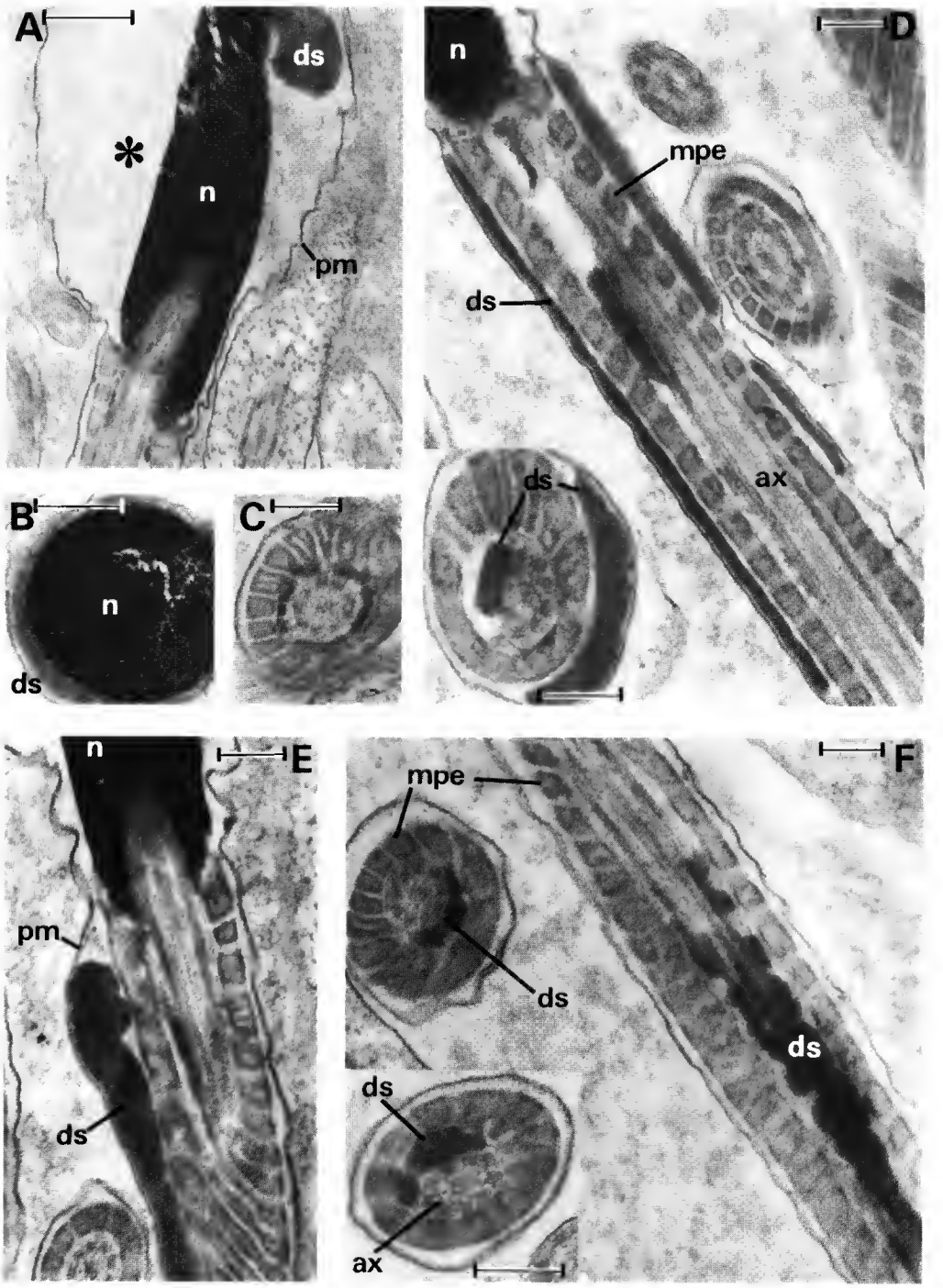

PLATE II

PLATE III

Alviniconcha : euspermatozoa and paraspermatozoa

A — L.S. junction of midpiece and glycogen piece showing annular complex.
B — T.S. junction of nucleus and midpiece (upper right), midpiece and glycogen piece.
C — L.S. junction of glycogen piece and end piece.
D — Paraspermatozoa. Note large vesicles pressed against each other, and occasional, highly electron-dense bodies (arrow). Inset showing three dense bodies within a common membrane.
E — Detail of dense body and portion of a large vesicle.

Scale bars : A-C = 0.5 μm; D-E = 1.0 μm.

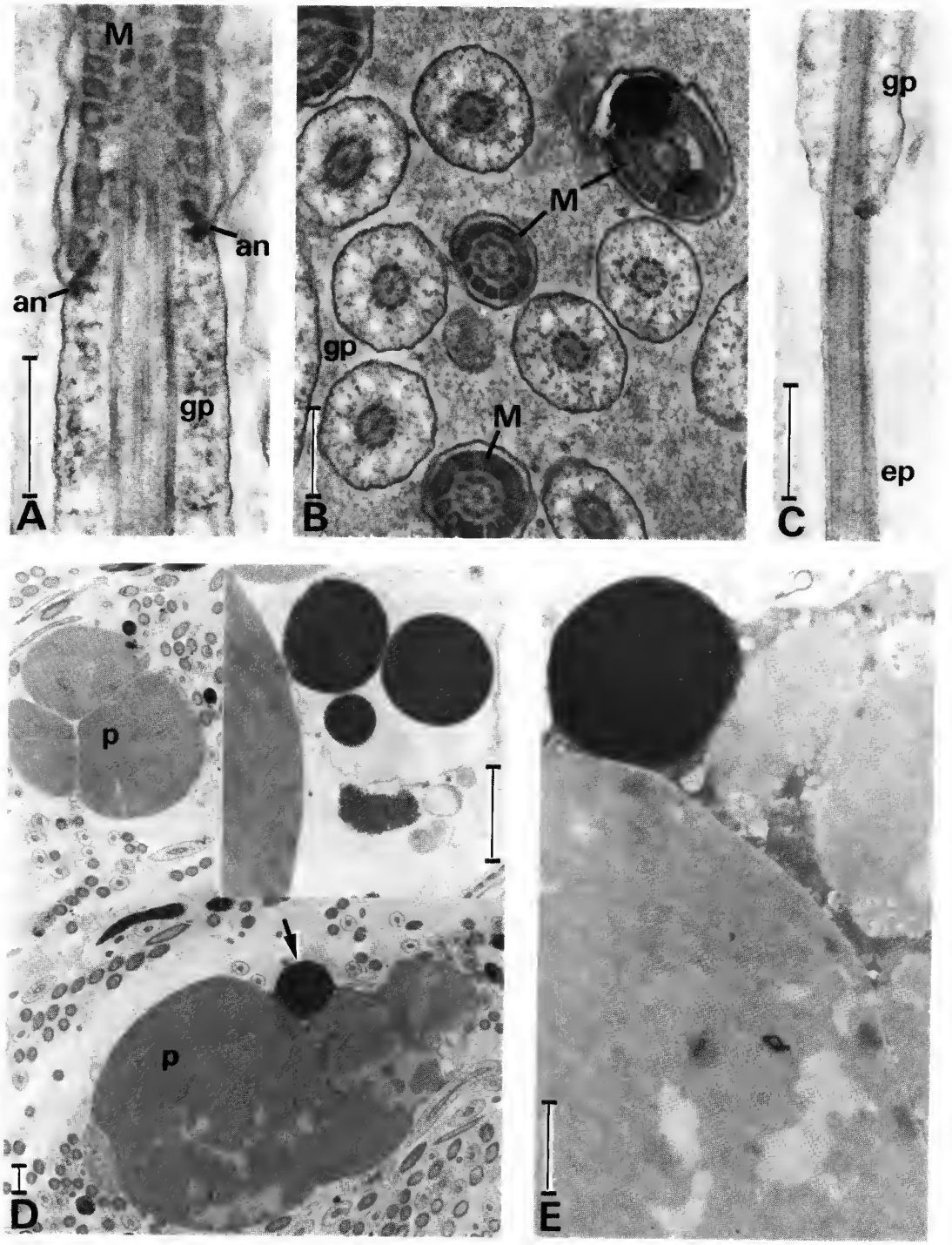

PLATE III

PLATE IV

Trichosirius inornatus : euspermatozoa and paraspermatozoa

A — L.S. through eusperm acrosomal complex and nuclear apex.
B — L.S. through eusperm nucleus-midpiece junction.
C — T.S. through eusperm nuclear apex and centriolar derivative.
D — T.S. eusperm midpiece showing 5-6 helical, mitochondrial elements.
E — L.S. junction of midpiece and glycogen piece showing annulus (2 rings) and helical mitochondrial elements.
F — T.S. eusperm nucleus (in region of centriolar derivative) and flattened anterior region of paraspermatozoon (note interspersed axonemes and mitochondria).
G — T.S. various regions of euspermatozoa and paraspermatozoa. 1-3 indicate anterior-posterior sequence through paraspermatozoa. Note spoke-like structures within the glycogen piece of euspermatozoa.

Scale bars : A-E = 0.25 μm; F = 0.5 μm.

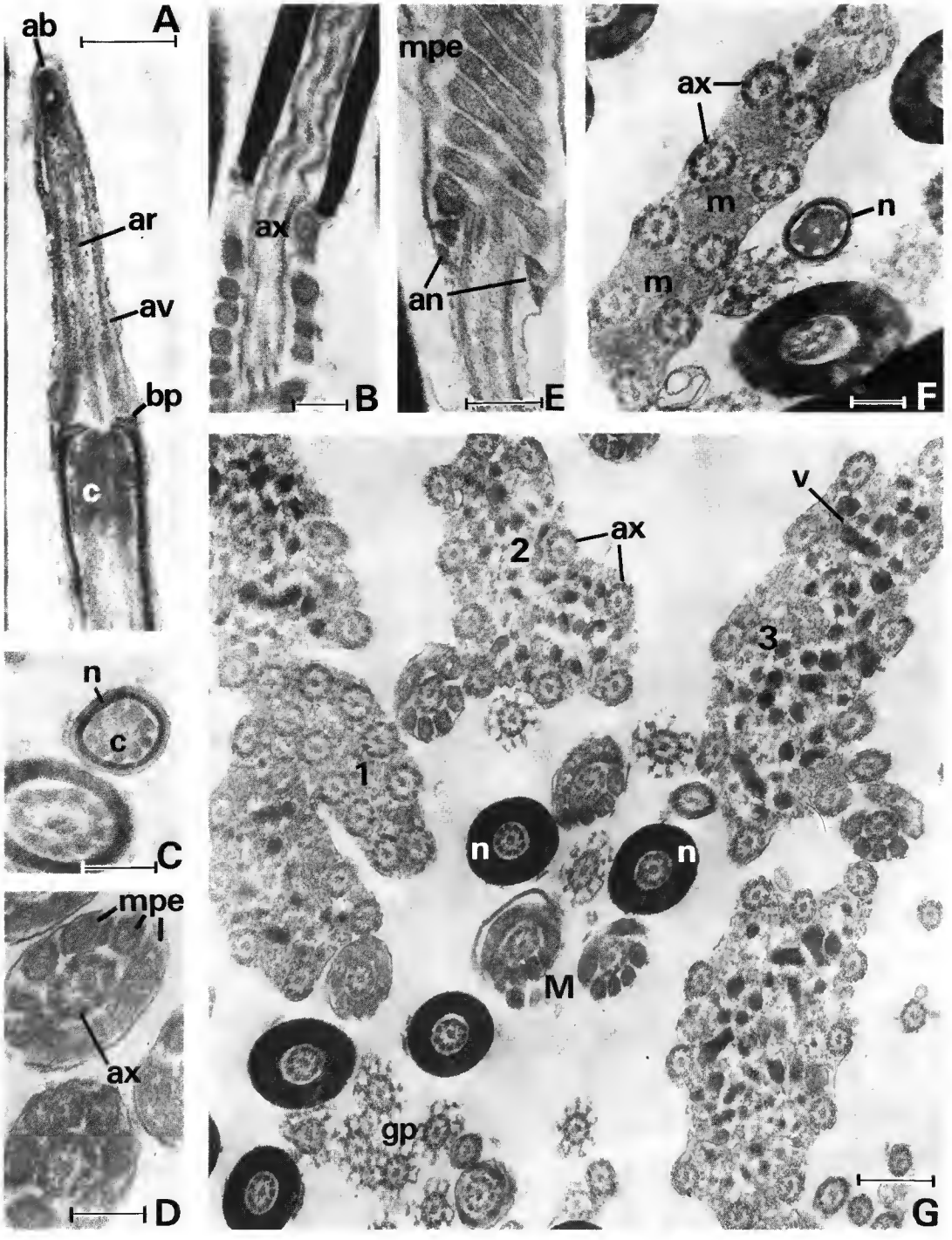

PLATE IV

Bull. Mus. natl. Hist. nat., Paris, 4e sér., **14**, 1992,
section A, n° 2 : 293-381.

Taxonomy of Tropical West African Bivalves
IV. Arcidae

by P. Graham Oliver and Rudo von Cosel

Abstract. — Twenty species of Arcidae are described from tropical West Africa, defined here as between 23° N and 17° S. The Arcinae are represented by four genera and include four new taxa : *Arca avellana turbatrix* n. subsp., *Barbatia gabonensis* n. sp., *B. ionthados* n. sp., *B.* (*Nipponarca*) *allocostata* n. sp. The anatomy of the latter is described and confirms the value of the subgenus which is redefined. The Anadarinae, other than *Senilia* and *Bathyarca* are all included in the genus *Anadara* because the use of the ligament orientation and inequivalve condition are abandoned as phyletic characters. Two new species are described : *Anadara eborensis* n. sp. and *A. camerunensis* n. sp. *A. polii* (Mayer) is the species often cited as "*A. diluvii* (Lamarck)" in publications concerning the Mediterranean. Variation within species is frequent, notably in *Anadara polii* and *A. senegalensis*. Ecological factors and geographical clines are invoked to explain some of this variation but local genetic isolation could not be excluded. The relationships of the shallow water West African species are analysed and compared to the faunas of the Mediterranean, Caribbean, Panamic and Indo-Pacific regions. Only one genus is endemic to West Africa, namely *Senilia*. There are three species common to the Mediterranean but none to the Caribbean although there are sibling species. Overall similarity is greatest with the Indo-Pacific but the Anadarinae in isolation have affinity to the Panamic fauna. A general discussion on the zoogeographical patterns for all the Arcoidea is presented in the concluding part of this study which is to be published in the next issue of the *Bulletin du Muséum*.

Résumé. — Description de vingt espèces d'Afrique occidentale tropicale, ici définie entre 23° N et 17° S. Les Arcinae sont représentés par quatre genres ; quatre taxa nouveaux y sont inclus : *Arca avellana turbatrix* n. subsp., *Barbatia gabonensis* n. sp., *B. ionthados* n. sp., *B.* (*Nipponarca*) *allocostata* n. sp. L'anatomie de la dernière est décrite, confirmant la valeur du sous-genre ici redéfini. Outre *Senilia* et *Bathyarca*, toutes les Anadarinae sont incluses dans le genre *Anadara*, car l'utilisation de l'orientation du ligament et l'inégalité des deux valves sont abandonnées en tant que caractères phylétiques. Deux espèces nouvelles, *Anadara eborensis* n. sp. et *A. camerunensis* n. sp. sont décrites. Dans des publications concernant la Méditerranée, *A. polii* (Mayer) a été souvent citée comme « *A. diluvii* (Lamarck) ». Une variabilité intraspécifique est fréquente, surtout chez *A. polii* et *A. senegalensis*. Des facteurs écologiques ainsi que des clines géographiques sont évoqués pour l'explication d'une partie de cette variabilité, mais on ne peut pas exclure d'une isolation génétique locale. Les espèces du plateau continental ouest-africain sont analysées sur le plan de leurs relations, et comparées avec les faunes de la Méditerranée, des Caraïbes, du Pacifique panaméen et de l'Indo-Pacifique. *Senilia* est l'unique genre d'Arcidae endémique de l'Afrique occidentale. Trois espèces vivent aussi en Méditerranée, mais aucune n'est présente dans les Caraïbes bien qu'il y ait des espèces jumelles. Les Arcidae dans leur ensemble présentent le maximum de similitude avec celles de l'Indo-Pacifique ; cependant les Anadarinae montrent une affinité plus marquée avec celles du Pacifique panaméen. Une discussion générale sur la répartition zoogéographique de tous les Arcoidea se trouve dans une deuxième partie de cette étude, qui sera publiée dans le prochain numéro du *Bulletin du Muséum*.

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Introduction

This paper on the Arcidae and the forthcoming second part on the Noetiidae (which also will contain the concluding discussion) are parts of a revision of the Bivalvia of tropical West Africa being undertaken by the second author and made possible by the availability of recent collections through ORSTOM (with main part of the fieldwork by the second author) and Serge Gofas (MNHN). The region is defined here as lying between Rio de Oro (southern part of West Sahara, 23° N) and Baia dos Tigres (Southern Angola, 17° S). Previous studies of the region are sparse with only the work of Dautzenberg (1909, 1913, 1927) and Nicklès (1950, 1955) of note. These papers illustrate the concept of shared taxa with the Caribbean and Mediterranean regions but the recognition of pan Atlantic species and local species appears to be inconsistent. For example the *Barbatia candida/complanata* complex was usually considered to be a single pan Atlantic species but the equally confusing *Arcopsis afra/adamsi* complex (cf. second part, Oliver and Cosel, *in print*) has always been regarded as two distinct species. Interestingly *A. afra* has also been widely cited from the Indo-Pacific. The actual relationships of such apparent circumtropical species complexes have never been elucidated. The aim of this review is therefore twofold : (1) To describe and illustrate all species of Arcoidea from tropical West Africa and (2) To examine the relationships of the west African species to those from the Caribbean, Mediterranean and Indo-Pacific.

In both parts, data on the morphometrics of the shells are frequently presented as box plots. The box represents the range of values of the first thirty percent of the sample either side of the mode, the projecting lines the next ten percent and the outlying points the remainder of the values. We have used these as we feel they give a rapid visual understanding of the range of values and the consequent variation. The box plots and all other descriptive and comparative statistics are derived from analyses using Statview SE™.

The general discussion on zoogeographical patterns is presented in the second and concluding part of this paper which will be published in the following issue of this Bulletin.

Abbreviations used in the text

BMNH : British Museum (Natural History) (now : The Natural History Museum), London, U.K.
MNHN : Muséum national d'Histoire naturelle, Paris, France.
NMWZ : National Museum of Wales, Dept. of Zoology, Cardiff, U.K.
SMF : Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt/M., Germany.
USNM : United States National Museum, Smithsonian Institution, Washington, D.C., USA.
ZMB : Zoologisches Museum der Humboldt-Universität Berlin, Berlin, Germany.
ZMC : Universitets Zoologisk Museum, Copenhagen, Denmark.

leg. : legit, collected by; sh. : shell, shells; spm. : specimen, specimens; sta. : sampling station; v. : valve; RV : right valve; LV : left valve.

Family Arcidae

Subfamily Arcinae

Genus **ARCA** Linné, 1758

Type species : *Arca noae* Linné, 1758 (SD Schmidt, 1818, ICZN Opinion 189).

Arca noae Linné, 1758
(Pl. I, 1A-1D, 2; fig. 1; map 1)

Arca noae Linné, 1758 : 693.
Arca despecta P. Fischer, 1876 : 258-259; pl. 8, fig. 1.

Type material : One marked specimen in the Linnean Collection in London (Dodge, 1952 : 143). The holotype of *Arca despecta* Fischer is in MNHN.

Type locality : "M. rubro, Mediterraneo, Indico" but now taken to be the Mediterranean. For *A. despecta* Fischer "littora Africae occidentalis" but the precise locality is not recorded.

Description

Shell to 90 mm in length. Equivalve. Inflated. Inequilateral, beaks in the anterior quarter.

Outline narrowly elongate, subtrapezoidal. Posterior area long and narrow usually slightly sulcate; posterior angle initially carinate, becoming rounded but remaining distinct; posterior margin sloping outwards, usually auriculate, may be subtruncate. Median sinus distinct in early stages but becoming obscure; ventral margin straight or sinuous usually indented at byssal gape. Anterior margin sloping inwards, more or less straight or gently curved. Dorsal margin very long, straight.

Dorsal area very long and may be extremely wide, more or less flat; umbonal separation great, umbos low. Ligament initially restricted to a triangular area between the beaks but developing to fill most of the dorsal area. Chevrons initially symmetrical but becoming irregular with numerous insertion sites.

Hinge plate very narrow; teeth in two series, separation obscure but just behind the line of the beaks. Anterior set up to 40 teeth, posterior set up to 60 teeth. Teeth minutely serrated, more or less straight and vertical.

Sculpture primarily radial of narrow ribs, riblets and raised threads. In juveniles there are 30-35 more or less uniform riblets. In adults posterior area with 2-3 subobsolete ribs; posterior angle becoming smooth; postero-median zone with 5-8 narrow ribs which are not much stronger than the 10-15 median riblets; anterior area with 4-6 riblets; all median and anterior zones with interspace raised threads.

Periostracum usually worn remaining around byssal gape and margins, composed of

fragile semidiaphanous straw coloured concentric lamellae with very weak radial thickenings; carinal bristles broad, irregular, laminar, rarely persistent.

External background colour cream to white overlain with closely spaced buff to rust brown oblique somewhat zigzag bands.

Adductor scars unequal, the posterior about twice the size of the anterior. Byssus retractor elongate, triangular, extending along three quarters of the posterior hinge plate.

SELECTED SHELL MEASUREMENTS : For ratios of length to height, length to tumidity and length to anterior to beak length, see figure 3 under *Arca bouvieri.*

DISTRIBUTION : Eastern Atlantic from southern Portugal (Lagos, Algarve (rare)) south to Senegal M'Bour, 14° N); Canary Islands, Cape Verde Islands; throughout the Mediterranean.

MATERIAL EXAMINED : **Mediterranean Morocco** : M'diq, on beach, 2 v., leg. GOFAS : Ceuta, Ensenada de la Almadraba, 20-26 m, 1 juv. v., leg. BOUCHET; south of Ceuta, 35°53′ N/05°19′ W, 50 m, 1 juv. v., leg. VON COSEL, both V.1986; Melilla, 1 sh., 2 v., coll. Staadt, all MNHN. **Algeria** : Beni Saf, 1 spm.; Oran, 6 spm., both coll. LOCARD, 1892; 3 sh., 1 v., coll. PALLARY, 1904; 3 v., old coll.; Alger, 1 sh., 2 v., old coll.; all MNHN. **Tunisia** : Sfax, 2 v., coll. LOCARD, 1892; NW of Bou Grara Sea, Gulf of Gabes, 1 spm., some juv. v.; Borj Djillidj, Djerba Island, 10 spm., Djerba, north coast, on beach, many v.; Canal d'Ajim, Djerba, 10-32 m, many spm., all leg. BOUCHET & WARÉN, 1982; all MNHN. **Greece** : Euboea Channel, 1 spm., coll. CHAPER, MNHN. **Italy** : Venice, 1 sh., coll. MONTEROSATO, 1906; Palerme, 1 sh., coll. ALLERY, 1872; Naples, 3 spm., coll. LOCARD, 1892; 2 sh., coll. PETIT, 1873; all MNHN. **Mediterranean France** : Cannes, Alpes-Maritimes, 1 spm., 2 sh., old coll. MNHN; St. Tropez, Var, 3 sh.; Porquerolles, Var, 1 sh.; Sanary-sur-Mer, Var, 1 sh.; Marseille, 3 sh.; St. Henri, Bouches-du-Rhône. 1 sh., all coll. LOCARD, 1892, MNHN. **Corsica** : St. Florent, 1 spm.; Bastia, 1 spm., both coll. LOCARD, 1892; Propriano, on beach, 1 v., leg. DELAUNAY; Ajaccio, 2 spm., coll. LOCARD, 1882; all MNHN. **Balearic Islands** : Mahon, Menorca, 5 spm., MELVILL-TOMLIN colln., NMWZ. Palma de Mallorca, 12 v., coll. SOYER, 1969, MNHN. **Mediterranean Spain** : Cadaques, Costa Brava, 3 sh., 1 v., leg. CHERRIERE, 29.VIII.1966; 5 spm., both old coll. MNHN. **Atlantic Morocco** : Tanger, 1 spm., 1 sh., coll. PALLARY, MNHN. **Canary Islands** : Las Palmas, Playa Alcaravaneras, 1 sh., 3 v., in the nets of fishermen; Playa Las Canteras, 5 v., both leg. VON COSEL, 1965, MNHN ex coll. VON COSEL. **West Sahara** : off Cap Barbas, 21°05′ N/17°14′ W, 43-45 m, 2 spm., 1 v., "Calypso"-Sta. 1, leg. MARCHE-MARCHAD, MNHN. **Mauritania** : Port-Étienne (now Nouadhibou), 2 spm., 2 sh., Mission GRUVEL; Pointe des Maures (20°55′ N), intertidal, 1 spm., leg. BOUCHET, V.1983; Pointe Cansado, 2 v., Mission GRUVEL, 5.IV.1908; all MNHN. **Cape Verde Islands** : (without precise locality) 1 v., coll. DE CESSAC, 1877; Santo Antão, Punta do Sal, 5 v., leg. CADENAT; São Vicente, Baia Matiota, Mindelo, 3 m, 3 juv. v., leg. VON COSEL, 16.XII.1978; Razo, on beach, 1 v., leg. SCHLEICH, VIII.1981; São Nicolau, Tarrafal, 1 v., leg. GROH, XII.1978; Ilha do Sal, Santa Maria, on beach, several juv. v.; Boavista, Sal Rei, 1 v.; Boavista, 1,4 miles W of Pta. Areia, 22 m, 4 v.; Boavista, off Praia Corralhino, 10 m, 1 v.; São Tiago, northern part of Baia de Sta. Clara, 15-35 m, 1 spm.; São Tiago, 14°54′ N/23°30,5′ W, 15 m, 1 v.; 15°16′ N/23°47′ W, 55-60 m, 1 v.; 15°13,2′ N/23°46,3′ W, 1 juv. v.; Fogo, SW of Sta. da Encarnacão, 20-25 m, 1 juv. spm., 10 m, 1 juv. ch. all dredged R/V "Calypso", leg. MARCHE-MARCHAD, XI.1959; all MNHN. **Senegal** : Banc de Seminole, 43-45 m, 1 juv. spm., 3 v., leg. MARCHE-MARCHAD; Dakar, Bel-Air, Plage de la Marine, 2 sh., 3 v., leg. VON COSEL, 16.X.1988; Dakar-Hann, on beach, 1 sh., 3 v., R/V "Président Théodore Tissier", littoral station, 1936; Gorée, 1 spm., leg. GUILBERT, 7.II.1958; SE of Gorée, 14°41′ N/17°23,3′ W, 17-19 m, 1 spm., 5 v., dredged R/V "Louis Sauger", leg. VON COSEL, 24.III.1988; Cap Rouge, several juv. sh., Mission GRUVEL, III-IV.1909 ; M'Bour, Petite Côte, on beach, 1 sh., 2 v., leg. VON COSEL, 22.III.1988; off M'Bour, 14°26,5′ N/17°05,5′ W, 10-11 m, 4 spm., 6 v.; off Saloum estuary, 14°2,5′ N/17°09′ W, 24 m, 2 v., both dredged R/V "Commandant Henri Gomis", leg. BODARD, 8.XII.1966; all MNHN. **Guinea** : Off Dubreka Estuary, 9°42′ N/15°33′ W, 35 m, 1 old valve which still shows colours; off Conakry, 9°30′ N/15°09,6′ W, 45 m, 1 old, apparently subfossil v.; off the border to Sierra Leone, 9°06′ N/14°35′ W, 52 m, 1 old, app. subfossil v.; all dredged R/V "André Nizery", leg. VON COSEL, 29-30.X.1988, all MNHN.

BIOTOPE : *Arca noae* lives mainly on hard grounds and is byssally attached on rocks, to the undersides of rocks and in crevices. On soft bottoms it can be found attached to isolated stones or other hard objects including the shells of larger gastropods. The bathymetric range is from low water to about 50 m.

REMARKS : See under *Arca bouvieri*.

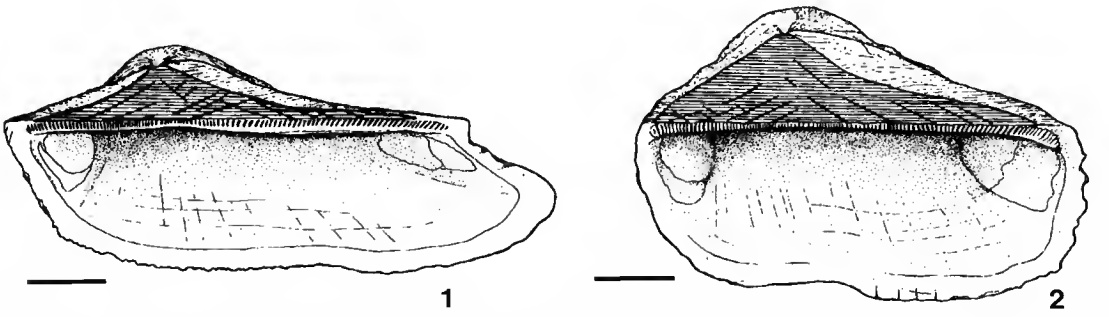


FIG. 1-2. — 1 : Internal view of right valve of *Arca noae* L. Western Sahara. 2 : Internal view of right valve of *Arca bouvieri* Fischer. Angola. (Scales bars = 10 mm.)

Arca bouvieri P. Fischer, 1874
(Pl. I, 3A-D, 4; fig. 2; map 1)

Arca bouvieri P. Fischer, 1874 : 206.
Arca sanctahelenae Smith, 1890 : 305, pl. 22, figs. 8-8b.

TYPE MATERIAL : The holotype (coll. BOUVIER) has not been isolated in the MNHN although ROCHEBRUNE (1881 : 250) cites it as "Sta. Vincent, Bouvier 1870, Mus. Paris." Two paratypes (complete specimens) from coll. PETIT DE LA SAUSSAYE are present and among them is the specimen figured by FISCHER (1876 : 239-240, pl. 8, fig. 2).

TYPE LOCALITY : Cape Verde Islands.

DESCRIPTION

Shell to 70 mm in length. Solid. Equivalve. Inequilateral, beaks in the anterior third. Outline subtrapezoidal, oblong, height relatively great. In large specimens : Posterior area relatively large; posterior angle rounded; posterior margin long, almost vertical, often straight some weakly auriculate. Median area as a shallow sinus, ventral margin more or less straight or with a shallow indentation at byssal gape. Anterior margin broadly rounded. Dorsal margin long, straight. In small specimens : Posterior area narrow; posterior angle carinate; posterior margin subacute, sloping inwardly, auriculate at junction with posterior carina. Median sinus marked; ventral margin indented. Anterior margin sloping inwardly, weakly indented. Dorsal margin relatively very long, lateral junctions acute.

Dorsal area long, very wide and almost flat rising gently to low umbos. Ligament initially restricted to triangular area between beaks but eventually covering most of the dorsal area except for a narrow posterior strip and a very narrow anterior strip. Chevrons developing symmetrically at first but in gerontic examples becoming irregular and often very numerous.

Hinge plate very narrow. Teeth in two series, junction just behind the beaks and indistinct. Anterior set up to 40, posterior set up to 50 in number. All teeth finely serrated, postero-median teeth slightly chevron shaped, remainder more or less straight and vertical.

Sculpture primarily radial of ribs, riblets and raised threads. Juveniles which about 30-35 more or less uniform riblets except for those on the posterior area which are much larger. In large specimens : posterior and postero-median area with 8-10 rounded ribs with up to 6 raised threads in the interspaces. Median area with numerous riblets and raised threads. Anterior area with 4-6 ribs.

Periostracum mostly worn, retained around margins only in adult examples. Composed of very thin, subdiaphanous, straw coloured concentric lamellae, very weakly reinforced by radial thickenings and breaking down over ribs to give an apparent radial arrangement. In juveniles the carinal bristles are occasionally preserved, these are greatly expanded, irregularly spathulate and extremely fragile.

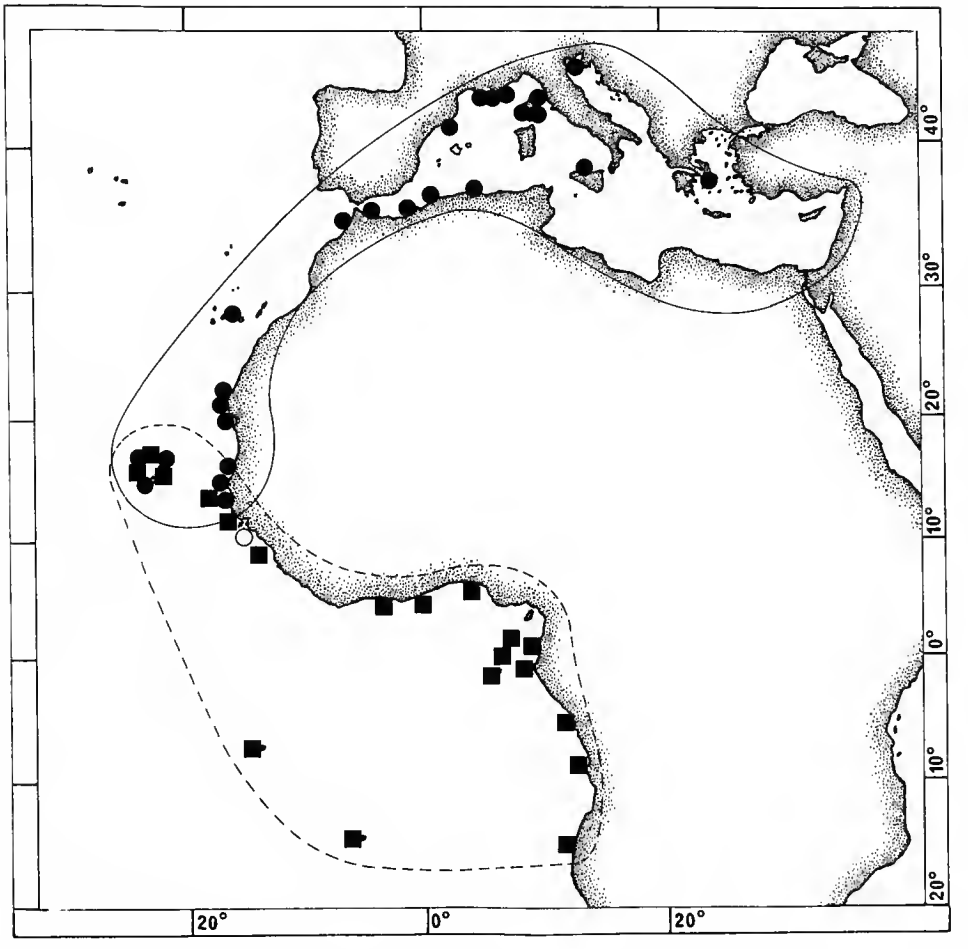
The external background colour of the shell is cream and is variously overlain with broad oblique, sometimes zigzag bands from brick red to purplish red in colour. Larger shells frequently have an orange tinge to the posterior area. Internal colour is mostly white except for a brickred marginal zone.

The adductor muscle scars are subequal, the posterior a little larger. The byssus retractor scar lies under the posterior part of the dorsal area, is an elongate triangle extending along two thirds of the posterior hinge plate.

SELECTED SHELL MEASUREMENTS : See in Remark section.

DISTRIBUTION : Senegal (Cape Verde Peninsula) to southern Angola (Moçamedes); Cape Verde Islands, São Tomé, Principe, Annobon; Ascension, St. Helena.

MATERIAL EXAMINED : **Senegal** : Dakar, SW of Madeleines Islands, 45-46 m, 3 juv. spm., 11 juv. v., leg. MARCHE-MARCHAD, 9.I.1954; Dakar, on Gouvernment Beach, 2 v., R/V "Président Théodore Tissier", littoral station, 1936; Dakar, SW of Cap Manuel, 50 m, 2 v., dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 20.II.1956; S of Gorée, 110-112 m, 1 juv. v., dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 18.II.1954; Gorée, 15-25 m, 11 spm., leg. PIN, 1987; Baie de Rufisque, 18-20 m, 1 juv. spm., 5 juv. v., Mission GRUVEL, II-IV.1909; off M'Bour, 14°2,5′ N/17°09′ W, 24 m, 6 spm., 1 v., dredged R/V "Commandant Henri Gomis", leg. BODARD, 7.XII.1966; M'Bour, on beach, 1 v., leg. VON COSEL, 22.III.1988; S-Casamance, off Cap Skirring, 12°25′ N/17°17′ W, 25 m, fine sand with stones, 1 spm., dredged R/V "Louis Sauger", leg. VON COSEL, 27.III.1988; all MNHN. **Cape Verde Islands** : (no precise locality), 1 sh., coll. DE CESSAC, 1874; São Vicente, 1 sh., 1 v., coll. MABILLE, 1905; S of Santa Luzia, 16°44′N/24°44,5′ W, 52 m, coarse sand with shells and stones, 1 juv. spm., 2 v., dredged R/V "Princess Alice II", 1901; Ilha do Sal, Pedra Lume, on beach, 1 juv. sh., coll. CADENAT; São Tiago, Praia, 14°53,7′ N/23°30,4′ W, 25-30 m, 4 juv. v., dredged R/V "Calypso", 17.XI.1959; Brava, SW of Punta Tantão, 20 m, 1 juv. v., dredged R/V "Calypso", 21.XI.1959; all MNHN. **Guinea** : off Rio Nuñez, 10°27′ N/15°37,5′W, 39 m, mixed sand with shells and gravel, 2 spm.; off Tannah Island, 9°12′ N/14°16′ W, 41 m, coarse sand with stones, 4 spm., several v., both dredged R/V "André Nizery", leg. VON COSEL, 28-30.X.1988, both MNHN. **Côte d'Ivoire** : off Abidjan, 5°01,5′N/3°23,5′ W, 70 m, sand



MAP 1. — Distribution of *Arca noae* (circles) and *A. bouvieri* (squares). The empty circle indicates a record of subfossil valves only.

with shells, 1 juv. v.; off Grand Bassam, 4°57′ N/2°42′ W, 40 m, 1 spm., 1 v., both dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, 19-22.III.1964, both MNHN. **Ghana** : Cape Coast, 26-31 m, 1 juv. spm., leg. LE LOEUFF, 10.II.1968; 4°36,5′ N/1°31′ W, 50 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 24.V.1956, both MNHN. **Nigeria** : off Niger Delta, 4°00′ N/6°11′ E, 34 m, 3 spm.; 4°03′ N/6°12′ E, 32 m, 10 juv. v., both dredged R/V "Calypso", 26.V.1956, leg. MARCHE-MARCHAD, both MNHN. **Ilha do Principe** : Between Pta. da Mina and I. Santa Ana, 10-12 m, 1 spm., 1 sh.; 1°42,5′ N/7°28′ E, 21 m, algues calcaires, 1 spm.; 1°43′ N/7°29′ E, 37 m, 1 spm.; 1°43′ N/7°28,4′ E, 73 m, 1 spm., 1 v.; 1°33′ N/7°31′ E, 90 m, 1 juv. spm.; all dredged R/V "Calypso", leg. MARCHE-MARCHAD, 24.VI-1.VII.1956, MNHN. **São Tome** : off Baia de Ana de Chaves, 5 m, calcareous algae, 1 spm.; off Praia Lagarto, 5-6 m, 1 spm.; off Diego Nuñes, 0°23′ N/6°43′ E, 30 m, 1 spm.; north coast,

0°25,5′ N/6°40′ E, 50 m, 1 juv. spm., all dredged R/V "Calypso", leg. MARCHE-MARCHAD, 11-21.VI.1956; all MNHN. **Annobon** : (without precise locality), 60 m, 3 juv. sh., coll. CAVELIER DE CUVERVILLE, 1886; north of Santo Antonio, 23 m, calcareous algae, 2 spm., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 4.VII.1956; all MNHN. **Equatorial Guinea** : Bata, 1 sh., coll. POBEGUIN, 1891, MNHN. **Gabon** : Pont-Gentil, Ile aux Pigeons, 3 m, on mangrove roots and *Pinna*, 5 spm., leg. CHEVALIER, 1984-89, MNHN. **R. P. Congo** : Pointe-Noire, plage Sauvage, 2 v., leg. VON COSEL, 10.XII.1985, MNHN. **Angola** : Barra do Dande, Bengo province, on rocks at low tide, 1 spm.; Cacuaco, Bengo province, on rocks at low tide, 1 spm.; 5-10 m, 9 juv. spm., 8 juv. v.; Ilha de Luanda, Luanda province, 40-60 m, 1 spm.; Corimba, Luanda province, 10-20 m, numerous spm.; Palmeirinhas, Luanda province, on rocks at low tide, 1 spm.; Cabo Ledo, Luanda province, 3 juv. spm., 3 juv. v.; Baia de Canoco, Benguela province, 2 juv. spm.; Praia Amelia, Moçâmedes, 40-60 m, 2 spm., all leg. GOFAS, 1981-86, MNHN.

BIOTOPE : Byssally attached on hard substrates such as rocks, stones, shell agglomerations and secondary hard substrates like shells or small stones on sand, mostly with calcareous algae. Bathymetric range from sublittoral to 60 m.

REMARKS

Arca bouvieri and *A. noae* have overlapping ranges only in the Senegal and Cap Verde regions. They can be separated at all sizes by the differences in shell shape (fig. 3) and sculpture. *Arca bouvieri* is less elongate, more compressed and less inequilateral than *A. noae*. The radial ribs of *A. bouvieri* are much stronger especially over the posterior area.

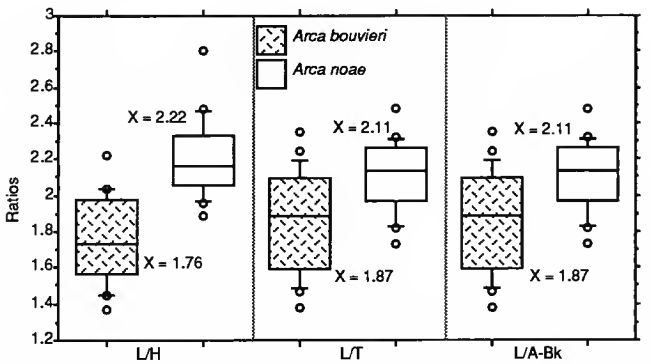


FIG. 3. — Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Arca bouvieri* (n = 20) and *Arca noae* (n = 20).

Arca bouvieri belongs to the *A. noae* group of species which is represented in the Caribbean by *A. zebra*, in the Indo-Pacific by *A. navicularis* and in the Panamic Pacific by *A. pacifica*. *A. bouvieri* differs from all of these in its relatively short quadrate outline and the large difference between the median and lateral sculpture. In these respects it differs most from *A. noae* and is closer to *A. zebra* and *A. navicularis*.

We can find no reason to regard *A. sanctahelenae* Smith as distinct from *A. bouvieri*. It

would appear that SMITH (1890) overlooked FISCHER's species as he compares the St. Helena material only with *A. noae* and *A. navicularis*. LAMY (1907 : 24) also considered *A. sanctahelenae* to be a synonym.

Arca avellana turbatrix n. subsp.
(Pl. II, 1A-D, 2; fig. 7; map 2)

TYPE MATERIAL : Holotype (28.3 mm), MNHN, Santo Antonio, Benguela province, Angola; intertidal, rocks; leg. GOFAS. Paratypes MNHN : 2 spm. as holotype; 2 spm. Lucira, Moçâmedes province, Angola; NMWZ : 8 spm. Corimba, Moçâmedes province, Angola; all leg. GOFAS.

TYPE LOCALITY : Santo Antonio, Benguela province, Angola.

DESCRIPTION

Shell to 35 mm in length. Equivalve. Inflated. Inequilateral, beaks in the anterior third. Outline subtrapezoidal, posterior area demarcated by a strong posterior angle which is often carinate. If small and not distorted then : longer than high; posterior margin obliquely truncate usually slightly auriculate, posterior ventral junction acute; ventral margin straight, gently curving or slightly indented by byssal gape; anterior margin broadly rounded; dorsal margin long straight, dorsal lateral junctions angular. Posterior area well demarcated by carinate posterior ridge, median sinus not apparent. If large then usually deformed to some degree and then : some remaining longer than high others almost as high as long; posterior margin obliquely subtruncate, posterior ventral junction angular or narrowly rounded; ventral margin variously indented byssal gape which may be extensive; anterior margin rounded, straight or irregular.

Dorsal area large, broadening rapidly with wide imbonal separation. Ligament extensive, covering dorsal area, chevrons irregular, developing rapidly and numbering up to 10 in gerondic specimens.

Hinge plate narrow, teeth small in two series but separation obscure, anterior set up to 38 teeth, posterior set up to 43 teeth. All teeth minutely serrated and with a frontal groove; posterior marginal teeth becoming chevron shaped, others straight and vertical.

Sculpture on posterior area of larger shells of 5-8 ribs, the first three from the posterior carina most prominent and usually at least one bifid. Towards dorsal margin ribs smaller, more variable in size, some as interspace riblets; of smaller shells usually of 4-5 simple ribs. Median area frequently divided by a weak posterior median ridge, posterior section with 15-20 nodulose riblets, anterior section and anterior area with 25-30 radial riblets variously with interspace radial threads. In most specimens the radial element is dominant but in more elongate examples the concentric element is equally expressed especially on the posterior median zone.

Periostracum rarely well preserved but usually present around byssal gape and remnants on posterior carina. Posterior carina with a single row of large, spathulate bristles which are smooth on the anterior edge and coarsely serrated on the posterior edge, they are thin, fragile and straw coloured (pl. II, 1A). On the posterior area short lamellar elements are present

between the ribs and are reinforced by weak slightly emergent hairs. On the remainder it is concentrically lamellar but breaks down into radially arranged segments which are weakly reinforced emergent hairs.

Shell generally pale in colour usually with mauve-brown tinges along the posterior border, occasionally extending throughout the posterior third, over the hinge plate and onto the anterior area, some darker brown on posterior area. Mantle pigmentation absent except for the black eyespots.

SELECTED SHELL MEASUREMENTS : See figure 4.

DISTRIBUTION : From Guinea (Conakry area) south to Cameroon and Angola (Luanda).

MATERIAL EXAMINED : **Senegal** : S of Cap Skirring, S-Casamance, 2 worn v., on beach, leg. VON COSEL, 3-6.III.1988, MNHN. **Guinea** : Roume, Iles de Los, beach on the N-side, 2 v., leg. VON COSEL, 29.V.1988; Kassa, Iles de Los, E-Side, N of village, on the undersides of boulders and stones with very thin layer of mud on them, low tide, 2 spm., leg. VON COSEL, 12.XI.1988, both MNHN. **Liberia** : 5°21,5′ N/9°54,5′ W, 73-80 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 20.V.1956, MNHN. **São Tome** : Praia Emilia, under stones at low tide, 1 spm., leg. GOFAS, XI.1983, MNHN. **Cameroon** : Victoria (now Limbe), Morton Bay, 2 spm., 1 v; Mondoleh Island, Ambas Bay, 6 spm., all under stones at low tide, leg. VON COSEL, IV.1969 and XI.1985, MNHN. **Gabon** : Cap Esterias-Pointe Idolo, on stones in sand at low tide, 3 spm., 1 v., leg. VON COSEL, MNHN; (no precise locality), 6 spm., coll. H. FISCHER, MNHN. **R.P. Congo** : Pointe-Noire, Plage ORSTOM, 3-6 m, many v.; Plage Mondaine, on beach, many v.; Songolo, 3-5 m, 3 v.; Plage Sauvage, on beach, 3 v., all leg. VON COSEL, XI-XII.1985; Pointe-Noire, 6 spm., 6 v., coll. Office Pte.-Noire; Pointe-Noire, 5 spm., coll. AUBERT DE LA RUE; all MNHN. **Angola** : Ambrizete, Zaïre province, 1 spm., 1 v.; Barra do Dande, Bengo province, 6 spm.; Cucuaco, Bengo province, 1 spm.; Praia Etambar, Corimba, Luanda province, 10 spm.; Caotinha, Benguela province, 4 spm., all leg. GOFAS, MNHN.

BIOTOPE : Byssally attached to stones and rocks, mostly on the undersides. This species appears to prefer more or less turbid waters and is also found in areas with slightly reduced salinities during the rainy season. Bathymetric range from low intertidal to sublittoral.

DERIVATIO NOMINIS : *turbatrix*, Latin, f. the "disturber" or "trouble maker" making reference to the systematic confusion prevalent in this group of species.

REMARKS

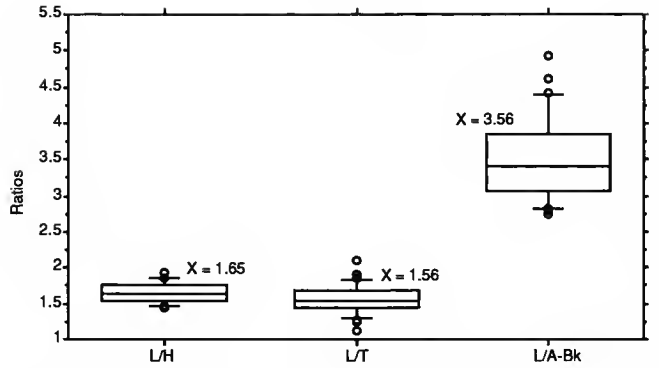
This is the tropical West African species referred to as *Arca imbricata* Bruguière of authors. Its identity has never been examined in any detail and it is assumed that it was identified as that species on geographical considerations alone. The distinctions between the Caribbean form known as *A. imbricata* and its Indo-Pacific counterpart. *A. avellana* Lamarck are similarly obscure. We have examined these in relation to the West African form and make the following observations :

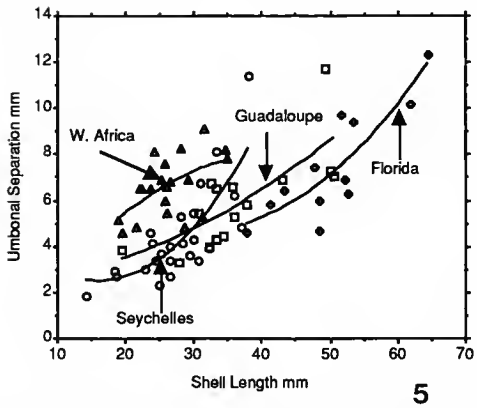
Character	Indo-Pacific	West African	Caribbean
Size	To 50 mm.	To 35 mm.	To 65 mm.
Posterior sculpture	Ribs often irregular, occasionally bifid.	Ribs often irregular, usually bifid.	Ribs mostly regular, rarely bifid
Periostracal insertion marks	Lacking	Lacking	Present
Ligament chevron N°	Medium	High	Low
Umbonal separation	Wide	Very wide	Moderate
Carinal bristles	Large, fragile straw coloured	Large, fragile straw coloured	Very large, robust greyish
Internal shell colour	Usually partly white	Mostly white	Usually dark overall
Mantle colour	Patterned shades of brown	White except for eye spots	Patterned shades of brown

Arca avellana (Indo-Pacific) (pl. II, 4) : This form has a larger maximum size but the general form of the shell, sculpture and periostracum are so similar that we are unable to identify significant differences. Only the umbonal separation and relative number of ligament chevrons show a difference (figs. 5 & 6). The colouration pattern is similar but there does seem to be a greater incidence of dark coloured specimens from the Indo-Pacific and this may also be reflected in the greater pigmentation of the mantle.

Arca imbricata (Caribbean) (pl. II, 3A-B) : The Caribbean form attains a much larger maximum size and in general is much less distorted. The shells are frequently more elongate and the ribs on the posterior area are rarely bifid but bear short grooves which represent the insertion points of the periostracal bristles. Umbonal separation is relatively small and the number of ligament chevrons is relatively fewer. The internal colouration is frequently darker with most specimens coloured throughout and many being chocolate brown or black. Most significantly however are the carinal periostracal bristles which are approximately twice the size, more strongly reinforced and more persistent (pl. IX, B).

From these comparisons it would appear that the West African form is more closely allied to that of the Indo-Pacific than it is to that of the Caribbean. However we have not addressed the possibility that these differences are merely ecophenotypic or of regional significance only. We suggest that as the total range of variation is not seen in all three groups that there is at least some regional significance. Even so this may reflect the absence of certain habitats in a region and in West Africa the exclusion of coral reef communities may be important. The habitats described here of the West African population are unusual in that the preference seems to be for turbid intertidal areas which are in contrast to the coral reef association with clear water in the tropical regions of the Caribbean and Indo-Pacific. Of the characters cited we view the carinal bristles to be most relevant as it is difficult to envisage the functional significance of the differences noted. The umbonal separation and ligament chevrons are related to growth with both having an allometric relationships to shell size (Thomas, 1976;





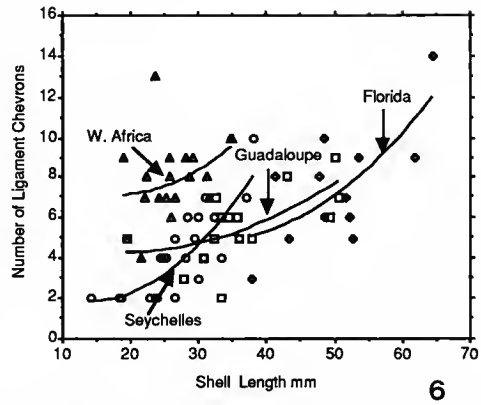


FIG. 4-6. — 4 : Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Arca avellana turbatrix* (n = 25). 5 : Graphs of Umbonal separation plotted against Shell Length for four samples of the *Arca imbricata* complex. Florida and Guadeloupe are *A. imbricata*, Seychelles is *A. avellana* and West Africa is *A. a. turbatrix*. 6 : Graphs of ligament chevron number plotted against shell length for four samples of the *Arca imbricata* complex. Florida and Guadeloupe are *A. imbricata*, Seychelles is *A. avellana* and West Africa is *A. a. turbatrix*.

OLIVER and ALLEN, 1980). The differences observed in these could be related to growth rate and if the West African population was restricted to less favourable conditions the allometry would then occur in the smaller size classes. The only meaningful way forward would be to carry out studies related to the genetic make up of each population but this is beyond the scope of the material at hand.

Resorting to traditional techniques we conclude that the West African form is most closely allied to that of the Indo-Pacific but the differences observed may be due to regional environmental conditions. However both populations are geographically isolated as the Indian Ocean populations do not spread beyond the province of Natal and the West African form is restricted to the Gulf of Guinea north of Namibia. Consequently we have given subspecific status to the West African form as *A. avellana turbatrix* but not in keeping with tradition regard it as distinct from the Caribbean form *A. imbricata*. If one views the differences to be insignificant then one cannot regard the Caribbean and Indo-Pacific forms to be distinct either

and neither would the distinction of the Panamic Pacific form known as *A. mutabilis* be justifiable. The whole complex would then have to be regarded as a single cosmopolitan species taking the earliest name of *A. imbricata* Bruguière. This is the position adopted by LAMY (1907 : 26-38) but he accepted three varieties within the Indo-Pacific ad West African ranges, namely var. *arabica* Philippi, var. *avellana* Lamarck, and var. *martensi* Dunker. He also isolated the Caribbean form as the nominate species *A. imbricata*.

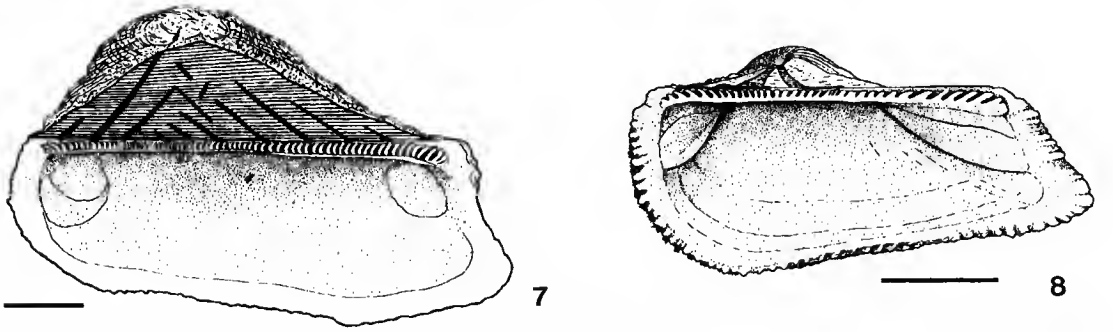


FIG. 7-8. — 7 : Internal view of right valve of *Arca avellana turbatrix* n. ssp. Angola. 8 : Internal view of right valve of *Arca retragona* Poli. Ireland. (Scales bars = 5 mm.)

Arca tetragona Poli, 1795
(Pl. II, 5A-B, 6; fig. 8; map 2)

Arca tetragona Poli, 1795 : 137.

TYPE MATERIAL : Not located.

TYPE LOCALITY : Sicily.

DESCRIPTION

Shell to 40 mm in length. Equivalve. Inflated if growth is unhindered but may be compressed if constricted in crevices. Inequilateral, beak position variable, in the anterior third in regular specimens but only just in front of the mid line in some distorted examples.

Outline subtrapezoisal, angular, juveniles elongate, adults irregular oblong. Posterior area narrow, well demarcated by the posterior angle which remains sharply carinate; posterior margin oblique, more or less straight, some very weakly auriculate. Median area not depressed, ventral margin gently curved or sinuate at byssal gape. Anterior margin rounded, variable. Dorsal margin long, straight.

Dorsal area wide to very wide, usually flat but may be cleft in distorted examples; umbos very low. Ligament with unusual growth pattern; initially with two strips of fibrous ligament radiating from the beaks, between these and to either side of them the dorsal area is free of ligament material. Lamellar chevrons are added mostly within the anterior strip then to the posterior strip and finally new sites of ligament growth appear along the hinge line between the

original strips so that in the largest shells most of the dorsal area is covered. The chevrons are very narrow and may reach 25 in number.

Hinge plate narrow, teeth in two series, separation obscure at a point behind the umbonal line; anterior set up to 30 teeth, posterior set up to 15 teeth. Teeth minutely serrated anterior teeth small, some chevron shaped, mostly vertical but marginal teeth oblique; posterior teeth straight but becoming progressively oblique towards the margin where they are subparallel.

Sculpture of radial riblets and raised threads, initially with 4-5 riblets on the posterior area and 30-35 finer riblets on the remainder, carinal riblet bifid often imbricate. Subsequently posterior riblets divide and are added to by interspace threads. Median area with closely spaced, somewhat acute riblets contrasting slightly with the more rounded and slightly broader riblets on the anterior area.

Periostracum usually lost, persistent around margins and on the posterior area only. Composed of concentric lamellae reinforced by bristles arising from the riblet interspaces, most often the lamellar part is worm and the arrangement appears simply radial. The bristles become spicate on the postero-median and posterior areas. The carinal bristles are large, lanceolate but with irregular margins. All the bristles are dark coloured from brown to black.

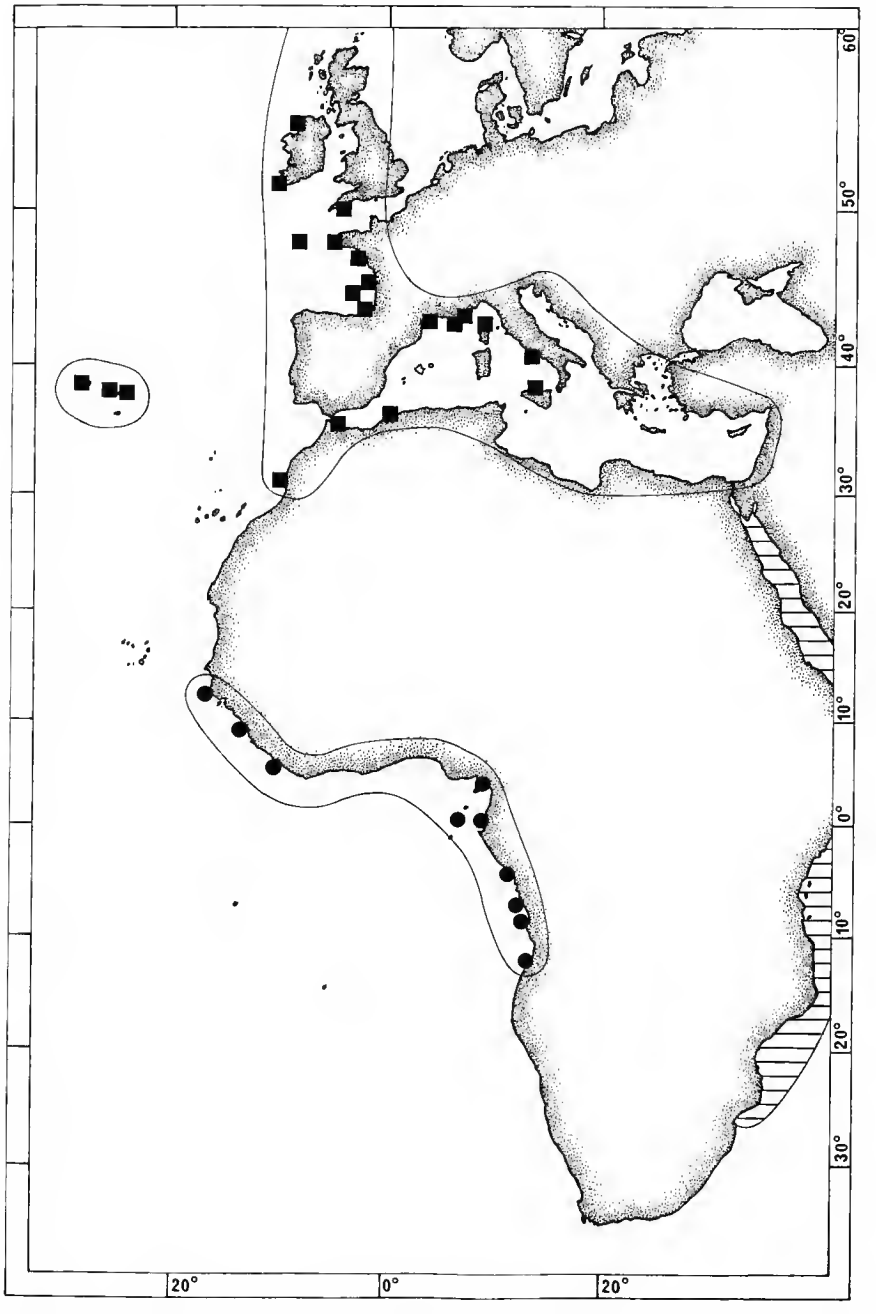
Shell colouration is weak, mostly greyish white but with some brown tinges internally over the posterior area.

Adductor scars small, subequal; both with myophoric ridges extending into the umbonal cavity. Byssal retractor small, triangular restricted to the posterior half of the shortened posterior hinge plate.

Distribution : Shetlands to Morocco (Essaouira/Mogador), the Azores and throughout the Mediterranean.

Material examined : **Ireland** : St. Johns Pt., Donegal, 5 spm., leg. P. G. Oliver, Berehaven, Bantry Bay, 9 spm., leg. J. T. Marshall; both NMWZ. **England** : Falmouth, leg. J. T. Marshall, 8 spm., NMWZ. **Celtic Sea** : 8 stations between 49°15′ and 48°33′ N and 05°09′ and 05°28,5′ W, 102-112 m, 15 v., all dredged R/V "Thalassa", leg. von Cosel, XII.1983, MNHN. **Atlantic France** : Brest, Finistère, 2 sh.; Lorient, Morbihan, 3 spm.; Belle-Ile, Morbihan, 1 sh.; Le Croisic, Loire-Atlantique, 4 spm.; Ile d'Yeu, Vendée, 2 spm.; Ile d'Oléron, Charente-Maritime, 3 spm., all. coll. Locard, 1982; Golfe de Gascogne (Biscay), 18 spm., coll. Denis; Arcachon, Gironde, 1 spm., coll. Roche, 1894; St-Jean-de-Luz, Basses-Pyrénées, numerous sh. and v., coll. H. Fischer, 1898; all MNHN. **Atlantic Spain** : Ceuta, Strait of Gibraltar, Punta Almina, 25-40 m, 6 spm., 1 v., leg. Bouchet, Gofas & Lozouet, V.1986, MNHN. **Algeria** : Oran, 40 m, 2 spm., 2 sh., coll. Pallary; 60 m, 3 spm., coll. Locard, 1892; Alger, 4 juv. sh., 1 v., old coll., all MNHN. **Italy** : Palermo, Sicily, 11 spm., 3 sh., coll. Jousseaume, 1916; 3 spm., 2 sh., coll. Allery, 1872; 7 spm., coll. Monterosato, 1906; Naples, 5 spm., 4 sh., coll. Petit, 1873; 4 spm., 2 sh., old coll.; 1 v., coll. Monterosato, 1906; Capri, 3 spm., coll. Locard, 1892; all MNHN. **Mediterranean France** : Nice, Alpes-Maritimes, 1 spm.; St. Raphaël, Var, 3 spm.; St. Tropez, Var, 2 spm., all coll. Locard, 1892; Toulon, Var, 1 spm., old coll.; Marseille, Bouches-du-Rhône, 9 spm., coll. Locard, 1892; 1 spm., coll. Vayssière, 1907; Sète, Hérault, 2 spm., coll. Locard, 1892; Banyuls-sur-Mer, Pyrénées-Orientales, 8 spm., coll. Lab. Arago, 1904; 4 spm., old coll., all MNHN. **Corsica** : St. Florent, N-coast, 2 spm., coll. Locard, 1892, MNHN. **Atlantic Morocco** : Mogador (now Essaouira), 6 spm., coll. Pallary, MNHN. **Azores** : Ponta Delgada, São Miguel, 10-20 m, 2 spm., 5 v., leg. Bouchet, 9-15.VII.1983, MNHN. 25 lots with numerous spm., sh. and v., from São Miguel, Terceira, Faial channel and Flores, between 39 and 225 m, empty shells and valves washed down on the steep slope to 1675 m, all dredged R/V "Jean Charcot", BIACORES-Expedition, leg. Métivier, X.1971, all MNHN.

Biotope : Byssally attached to rocks in crevices or in more open situations in tranquil sites such as those at depth. Bathymetric range from low in the intertidal to 100 m.



MAP 2. — Distribution of *Arca avellana turbatrix* (circles), *A. a. avellana* (shaded area) and *A. tetragona* (squares).

REMARKS : This species probably cannot be considered to be a component of the tropical West African fauna but as it can be confused with *Arca avellana turbatrix* and juveniles of *Arca noae* we have included it here. Even when distorted it can be easily separated on the form of the ligament and periostracal bristles.

Genus **ACAR** Gray, 1857

TYPE SPECIES : *Arca gradata* Broderip and Sowerby, 1829 (SD Woodring, 1925).

Acar cf. **plicata** (Dillwyn, 1817)
(Pl. II, 7A-B; fig. 10; map 3)

Arca plicata Dillwyn, 1817 : 227-228.

TYPE MATERIAL : Based on the figure in CHEMNITZ (1795 : 244, pl. 204, fig. 2008).

TYPE LOCALITY : Red Sea.

DESCRIPTION

Shell to 26 mm in length. Equivalve. Initially slightly compressed but soon becoming rather tumid to very tumid in gerontic specimens (the onset of the gerontic expansion can occur in a wide range of sizes). Inequilateral, beaks in the anterior 1/4 rather low.

Outline subrectangular-subtrapezoidal, anteriorly usually slightly narrowed; frequently distorted especially in gerontic examples. Posterior area narrow, demarcated by a persistent posterior carinal ridge; posterior margin oblique, posterior ventral junction subacute. Median area flat to weakly sulcate; ventral margin more or less straight but often sinuous; byssal gape obsolete or very narrow. Anterior area small, demarcated by a rounded ridge; anterior margin broadly rounded. Dorsal margin straight.

Dorsal area usually very narrow, wider anterior to the beaks but becoming wide overall in gerontic specimens; umbonal separation usually slight. Ligament restricted to well behind the beaks, chevrons very narrow, numbering up to 8 in normal specimens but as many as 20 in gerontic examples.

Hinge plate narrow to moderate, teeth in 2 series but separation obsolete except in old specimens where ligament growth has eroded the small central teeth; anterior set up to 10 teeth, posterior set up to 15 teeth. Teeth strong, anterior laminar, posterior chevron shaped, all coarsely serrated, marginal teeth becoming very oblique. In gerontic specimens the teeth may be irregular, often divided medially.

Sculpture imbricate, of up to 30 rather broad concentric ridges dissected by 25-35 radial ribs these dividing during growth to number up to 50. The resulting vesicular nodes are smoothly rounded except on the posterior angle where they may be incomplete and therefore slightly plicate. The posterior area bears 5-7 strong ribs on which the nodes are greatly swollen

giving the cross section of the posterior margin a strongly corrugated appearance. This is a little less so for the Cape Verde Islands material.

Periostracum very thin, rarely retained.

Shell whitish, exterior rather dirty cream; interior of Cape Verde, São Tomé and Annobon specimens mostly flushed with pale orange/pink, the Angolan material rarely so.

Adductor scars more or less equal, raised with myophoric flanges along their inner edges. Inner lateral margins crenulate, ventral margin weakly so or irregularly denticulate.

SELECTED SHELL MEASUREMENTS : See figure 9.

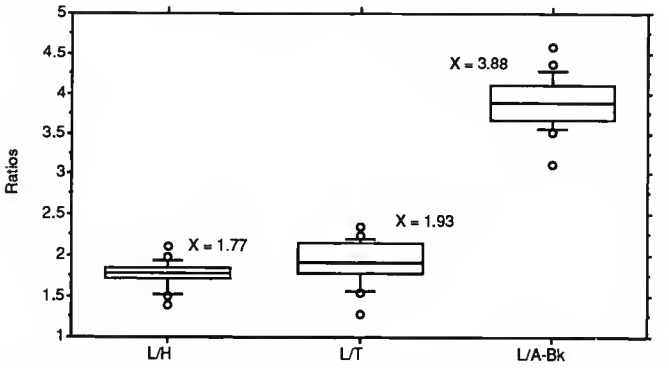
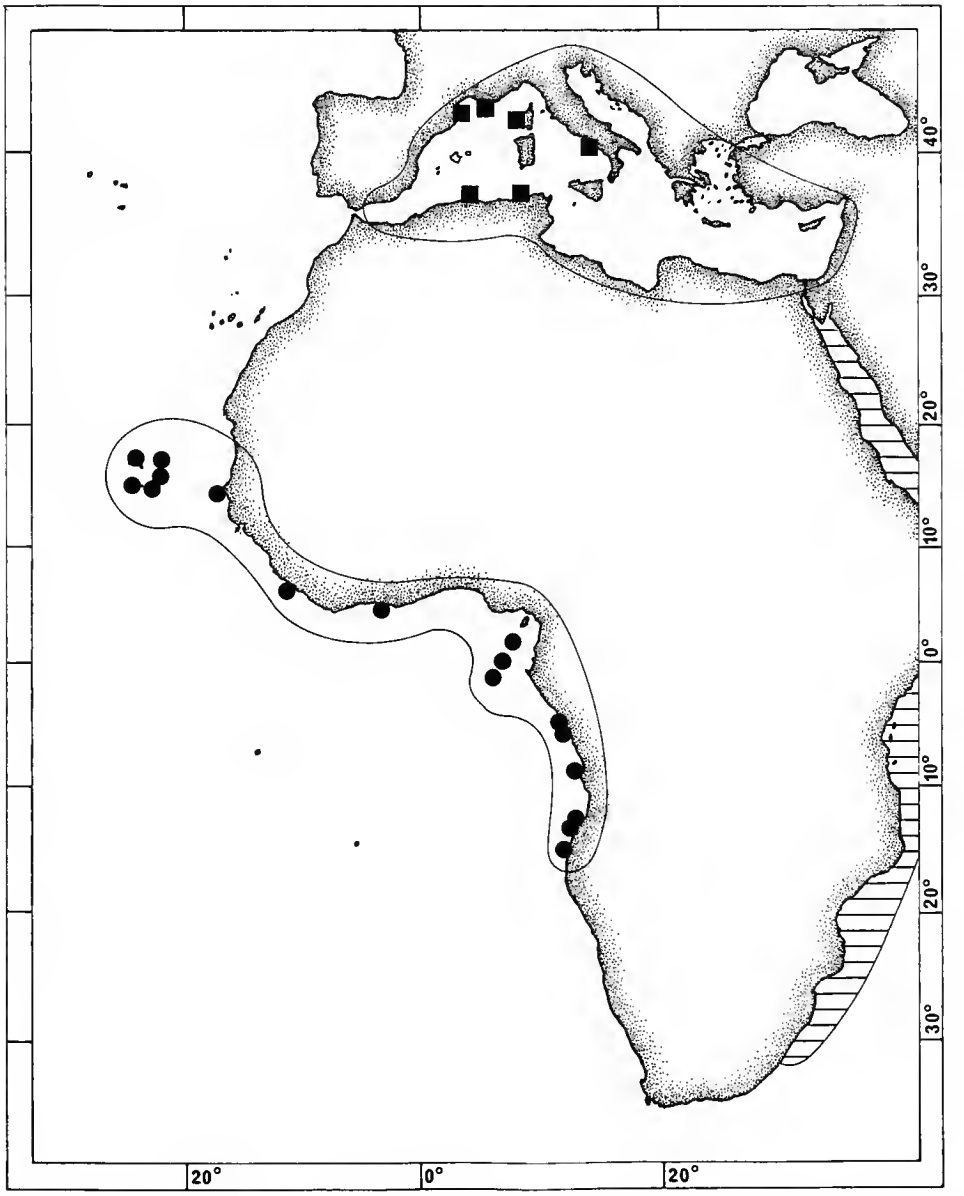


FIG. 9. — Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Acar* cf. *plicata* from West Africa (n = 24).

DISTRIBUTION : This species occurs from the Cape Verde Islands south to Angola but it is most common on the Cape Verde Islands, the islands in the Gulf of Guinea and on the coast of Angola.

MATERIAL EXAMINED : **Cape Verde Islands** : (no precise locality), numerous spm. and v., leg. RANG, 1837; 4 spm., coll. DE CESSAC; 5 spm., coll. BOUVIER; Santo Antão (no precise locality), 5 v.; São Vicente, Baia Matiota, Mindelo, on the undersides of stones, 1-2,5 m, 3 spm., 2 v.; São Vicente, Baia Porto Grande, 2 sh., 10 v., both leg. VON COSEL, XII.1978; Ilha do Sal, (no precise locality), numerous spm., sh. and v., leg. CADENAT, 1950; Ilha do Sal, Palmeira, undersides of rocks at low tide, 7 spm.; Ilha do Sal, Baia Algodoeiro, on beach, 4 v.; Ilha do Sal, Santa Maria, underside of boulders 2-3 m, 3 spm., all leg. VON COSEL, 15.XII.1978-1.I.1979; Ilha do Sal, 16°35'N/22°55' W, calcareous algae, 15 m, 1 spm., dredged R/V "Calypso", 26.XI.1959; Boavista, Gatas (Punta Rodrigo), on the undersides of stones on mixed sand, 1,5-2 m, 6 spm., leg. VON COSEL, 27.XII.1978; São Tiago, Praia, 8 v., leg. CADENAT, 1950; São Tiago, Porto de Praia, four lots with 3 spm. and 7 v., from 2 to 30 m, all dredged R/V "Calypso", 17-19.XI.1959; Brava SW of Punta Tantão, 20 m, 3 v.; Fogo, SW of Santa da Encarnacão, 20-25 m, 12 spm.; Fogo, Punta da Araia, 2.5 m, 2 spm. both dredged R/V "Calypso", 20.XI.1959; all MNHN. **Senegal** : Dakar, SW of Cap Manuel, 50 m, 1 v.; Dakar, 129-150 m, 1 v., both dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 1956 and 1958, MNHN, **Liberia** : 5°21,5' N/9°54,5' W, 73-80 m, 4 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 20.V.1956, MNHN. **Côte d'Ivoire** : Abidjan region (no precise locality), 2 v., leg. LE LOEUFF, MNHN. **Ilha do Principe** : W-coast, 1°37' N/7°22' E, 30 m, 1 v.; Baia de Santo Antonio, between Punta da Mina and Punta de Novo Destino, 6 m, 1 v.; Baia Santo Antonio, between Punta da Mina and Ilheu Santa Ana, 10-12 m, 1 spm.; both dredged R/V "Calypso", leg. MARCHE-MARCHAD, VI.1956, MNHN. **São Tome** : Punta Diogo Vaz, west coast, 30 m, 1 spm.; 1°38,4' N/7°22,1' E, 31 m, 1 spm.; off S. Tomé city, 0°20' N/6°45' E, 10 m, 2 spm., 5 v.; off Praia Lagarto,



MAP 3. — Distribution of *Acar* cf. *plicata* (circles), *A. plicata* (shaded area) and *A. pulchella* (squares).

5-6 m, 5 spm., all dredged R/V "Calypso", leg. MARCHE-MARCHAD, 11-27,VI,1956; all MNHN. **Annobon** : N of Santo Antonio, 23 m, 1 spm.; 1°25,2′ S/5°36,1′ E, 20 m, 1 spm., both dredged R/V "Calypso", leg. MARCHE-MARCHAD, VI and VII.1956; 1°24′ S/5°37,5′ E, 20-40 m, 1 spm., 1 v., leg. CROSNIER, 11.XII.1965; 1°28,5′ S/5°37,5′ E, 35-55 m, 3 spm., leg. POINSARD, 16.VI.1967; all MNHN. **R.P. Congo** : Pointe-Noire, Plage Mondaine, N of lighthouse, low tide, 7 v.; Plage Sauvage, on beach, 1 v.; Plage ORSTOM, coarse sand and stones, 5-7 m, 1 v., all leg. VON COSEL, XI-XII.1985, all MNHN; Loango, 4 v., leg. Office Pointe-Noire, 1969, MNHN. **Angola** : Cabo Ledo, Luanda province, 10-40 m, 2 spm.; Praia Etambar, Corimba, Luanda province, rocks, infralittoral, many spm.; Baia do Mussulo, Luanda province, 5 spm.; Baia de Santa Maria, Benguela province, rocks, 0-2 m, 18 spm.; Caotinha, Benguela province, rocks, infralittoral, 7 spm.; Baia do Limagem, Benguela province, rocks, 0-2 m, 1 spm.; Baia de Lucira (Bissonga), Moçâmedes province, intertidal, 4 spm.; Lucira (Praia do Cesar), Moçâmedes province, infralittoral, 3 spm.; Baia das Pipas, Moçâmedes province, rocks, 2 spm.; São Nicolau, Moçâmedes province, intertidal, 3 spm.; Praia Amelia, Moçâmedes province, rocks, infralittoral, 2 spm., all leg. S. GOFAS, 1982-1984, MNHN.

BIOTOPE : This species lives in crevices and under rocks where it is attached by a weak byssus. It is found from low in the intertidal to 40 m.

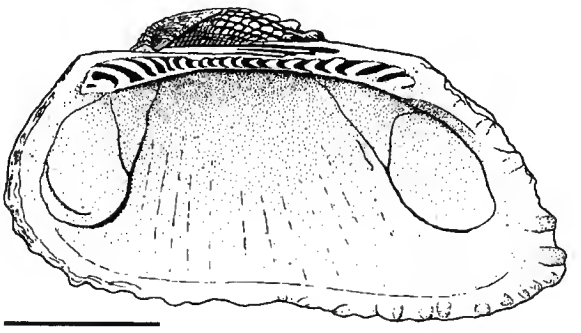


FIG. 10. — Internal view of right valve of *Acar* cf. *plicata* (Dillwyn). São Tomé. (Scale bar = 5 mm.)

REMARKS

The genus *Acar* is distinctive with its coarse imbricate sculpture and raised muscle scars but the species systematics are very complex. Traditionally the species are identified on their geographic distribution such that *A. plicata* is Indo-Pacific, *A. pulchella* (Reeve, 1844) is Mediterranean, *A. domingensis* (Lamarck, 1819) is Caribbean and *A. gradata* (Broderip & Sowerby, 1829) is Panamic. The West African form has been known by all but the Panamic name. ROST (1955) in discussing *A. gradata* mentioned the coarse and fine sculptured varieties of that species and we have observed the same feature in the Caribbean *A. domingensis* but not to any great extent in the West African form. Even in the coarse sculptured form of *A. domingensis* the nodes never appear to be so inflated as in the West African material and the posterior ribs are finer or lower. The orange/pink colouration is apparently absent from Caribbean material. In sculptural coarseness the Indo-Pacific *A. plicata* is very similar but generally as the name implies the concentric elements are more lamellar especially on the posterior angle which often appears foliate. The posterior ribs are similar in development but

again the nodes are not inflated or entire but are rather the form of domed plications. As with the West African form the frequency of orange/pink shells is rather great. *Acar pulchella* (pl. II, 8A-B) from the Mediterranean is a small species rarely exceeding 15 mm and differs from all others in that the sculpture is primarily of fluted, concentric, slightly elevated lamellae.

The distinctions rest therefore on the coarseness of the sculpture and the degree to which the radial and concentric elements fuse into either vesicular nodes of fluted lamellae. Given the great range in variation we are refraining from giving the West African material separate nomenclatural status. From our observations the similarities in coarseness of sculpture, distinctiveness of the posterior ribs, size and colour we conclude that the West African form is closer to that of the Indo-Pacific. MEYER (1868) in discussing the Tertiary forms of *Acar* suggested that *A. clathrata* (Defrance, 1816) was replaced by the Recent *A. pulchella*. In general form the Pliocene species is close to *A. plicata* and could also be the fossil equivalent of the West African form. We recognise the affinity of the West African and Indo-Pacific forms by using the name *A. plicata*.

Genus **BARBATIA** Gray, 1842

TYPE SPECIES : *Arca barbata* Linné, 1758 (SD Gray, 1857).

Barbatia complanata (Bruguière, 1789)
(Pl. III, 1A-B, 2, 3, 4, 5A-B; fig. 6; map 4)

Arca complanata Chemnitz, 1784 : 198, pl. 55, fig. 544.
Arca complanata Bruguière, 1789 : 100.
Arca stigmosa Dunker, 1853 : 46, pl. 9, figs. 8-11.

TYPE MATERIAL : The type is based on the figure given by CHEMNITZ (1784) and the specimen may be in the ZMC, Copenhagen. The type of *A. stigmosa* is probably in ZMB Berlin.

TYPE LOCALITY : This is cited as "Guinea" by CHEMNITZ which refers to tropical west Africa. BRUGUIÈRE cites Madagascar and O. Americano but this is erroneous and arises from the early belief that there was only a single pan-tropical species.

DESCRIPTION

Shell to 50 mm in length but usually not exceeding 35 mm. Equivalve. Compressed. Inequilateral, beaks in the anterior third.

Outline subrectangular-subtrapezoidal, often somewhat distorted (some to the extent of being subtrigonal), the anterior usually a little narrower. Posterior area poorly demarcated by a low weakly angled posterior ridged but more noticeably by the change in the size of the ribs; posterior margin oblique, more or less straight to gently curved, posterior ventral junction roundly subacute. Median area weakly sulcate; ventral margin subparallel to dorsal margin to inclined towards the anterior, more or less straight or indented or distorted especially at byssal

gape which is rather long but not very wide. Anterior area small, demarcated by a weak rounded ridge, anterior margin broadly rounded but often restricted and the oblique, slanting inwards. Dorsal margin long, straight.

Dorsal area narrow to very narrow, becoming deeply cleft, umbonal separation slight. Ligament initially opisthodetic, rapidly the dorsal area and extending anteriorly well beyond the beaks; chevrons narrow, numerous in gerontic specimens, numbering up to 12.

Hinge plate rather narrow especially centrally, teeth in two series which are almost inseparable, total teeth count up to 45. Central teeth very small, often destroyed by ligament incursion, lateral teeth laminar or chevron shaped, becoming strongly oblique.

Sculpture of numerous radial riblets and ribs; posterior area with 6-7 large ribs often with 1-3 small secondary riblets. In some, the primaries are bifid, not greatly elevated, well spaced and evenly dissected giving the appearance of a twisted rope; anterior and median areas with 55-60 primary riblets, the anterior and those adjacent to the posterior angle a little larger than the more closely spaced median riblets, posterior median riblets bifurcating at an early stage. All radial elements dissected by concentric element and therefore appearing nodulose, concentric element also present as widely spaced low ridges caused by the enlargement of the nodules at regular intervals, these correspond with the concentric rows of larger periostracal bristles.

Periostracum with a primarily concentric arrangement of raised lamellae strengthened by slightly emergent bristles arising from the interspaces; the lamellae usually break down into rectangular sections to give a frilled appearance; lamellae pale straw coloured, emergent bristles brown giving a very characteristic pattern.

Shell white.

Adductor scars subequal the posterior a little larger, posterior pedal/byssal retractor scar small, elongate. Inner margin finely crenulate.

SELECTED SHELL MEASUREMENTS : See figure 11.

DISTRIBUTION : This species ranges from Guinea (Conakry area) and the Cape Verde Islands (where it is rare) south to southern Angola and is also found in São Tome, Principe and Annobon.

MATERIAL EXAMINED : **Cape Verde Islands** : Ilha do Sal (no precise locality), 1 dwarf spm., leg. CADENAT, IV-VI.1950, MNHN. **Guinea** : Kassa, Iles de Los, E-side, N of village, on the underside of a stone, at low tide, 1 spm., leg. VON COSEL, 12.XI.1988, MNHN. **Liberia** : 6°40′ N/11°23′ W, 51 m, 1 juv. v. dredged R/V "Calypso", leg. MARCHE-MARCHAD, 19.V.1956, MNHN. **Côte d'Ivoire** : off Tabou, 4°16,5′ N/7°30′ W, hard bottom, 40 m, dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, 8.IV.1964; Abidjan region, "Palm Beach", on rocks, 6-10 m, 1 spm.; Canal de Vridi, Abidjan, 6 spm., 1 sh., 3 v.; Abidjan, SE of "2 Poteaux", on sandstone, 37 m, 1 juv. spm., all leg. LE LOEUFF, 1967-1973; all MNHN. **Ghana** : Cape Coast, hard bottom, 26-31 m, 1 spm., leg. LE LOEUFF, 10.II.1968; 4°37′ N/0°50′ W, 90-100 m, 3 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 24.V.1956, both MNHN. **Togo** : 6°10′ N/1°37′ E, 19 m, 2 juv. spm., leg. CROSNIER, 26.VII.1964, MNHN. **Benin** : Ouidah, 6°10′ N/2°05′ E, 100 m, 5 juv. v., leg. MARCHE-MARCHAD, 22.XI.1958, MNHN. **Nigeria** : off the Niger delta, 4°00′ N/6°11′ E, 34 m, on *Chama*, 1 juv. spm., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 26.V.1956, MNHN. **Cameroon** : Victoria (now Limbe), Morton Bay, E-side, between rocks at low tide 14 spm., leg. VON COSEL, 1-3.XII.1985; Mondoleh Island, Ambas Bay, under and between stones near low tide, numerous spm., leg. VON COSEL, IV.1969; Kribi, on beach, 8 v., leg. NICKLÈS, 1947; 3 spm., leg. VON COSEL, IV.1969; off Kribi, 2°36,8′ N/9°46′ E, 1 spm.; 2°33,3′ N/9°42,6′ E, 1 spm., both leg. CROSNIER, XII.1962; all MNHN. **Ilha do Principe** : Baia de Santo Antonio, 6-15 m, 4 spm., 1 sh., 8 v.; Baia das Agulhas, 4-8 m, 1 spm.; 1°37′ N/7°22′ E, 30 m, 3 juv. v.; 1°42′ N/7°28,8′ E, 37 m, 1 spm.;

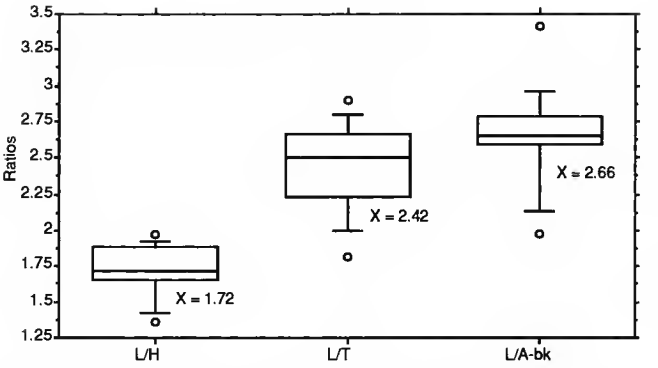
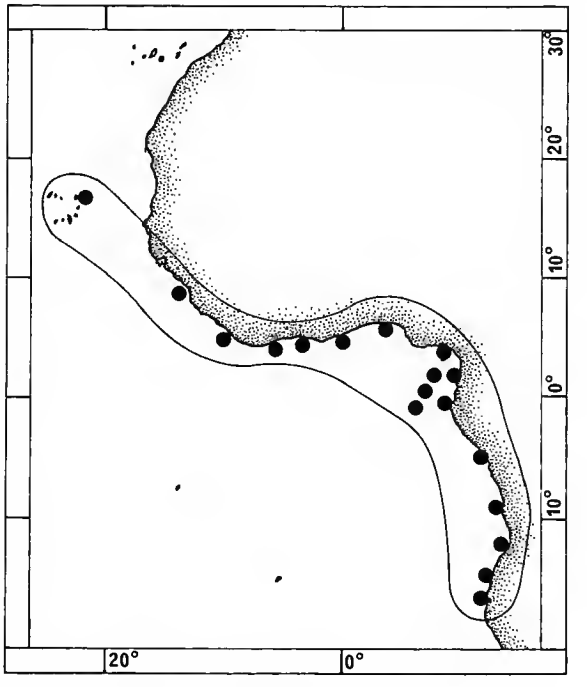


FIG. 11. — Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Barbatia complanata* from West Africa (n = 14).



MAP 4. — Distribution of *Barbatia complanata*.

1°20,7′ N/7°17,6′ E, 25-40 m, 1 dwarf spm., all dredged R/V " Calypso ", leg. MARCHE-MARCHAD, 25.VI-1.VII.1956; all MNHN. **São Tome** : Esprainha, near Neves, 3 spm.; Praia Morro Peixe, 1 spm.; Praia das Conchas, 2 spm.; Praia Emilia, several spm., all between and under rocks at low tide, leg. GOFAS, XI.1983; Punta Diego Vaz, 0,6 m, 3 spm.; Ilheu das Cabras, 1 sh., off Pta. Diogo Nuñes, 4 m, 1 spm.; off Praia Lagarto, 5-6 m, 4 spm., 5 juv. v., all R/V " Calypso ", leg. MARCHE-MARCHAD, 6-11.VI.1956; all MNHN. **Annobon** : 1°24′ S/5°37,5′ E, 20-40 m, 2 spm., leg. CROSNIER, 11.XII.1965; 1°24′ S/5°36,7′ E, 10 m, 1 spm.; 1°25,2′ S/5°36,1′ E, 20 m, rocks with calcareous algae, 2 spm., both dredged R/V " Calypso ", leg.

MARCHE-MARCHAD, 13.VI.1956; all MNHN. **Gabon** : off Port-Gentil, on oil platform anchor, 30 m, 1 spm., leg. CHEVALIER, 1987; Port-Gentil, 2 spm., coll. Office Pte-Noire, both MNHN. **R.P. Congo** : Pointe-Noire, Plage Mondaine, on beach. 1 v., leg. VON COSEL, XII.1985, MNHN. **Angola** : Cabo Ledo, Luanda province, 10-40 m, 1 sh.; Caotinha, Benguela province, 10 spm., 1 sh.; Baia Azul, Benguela province, rocks at low tide, 4 spm., 1 sh.; Baia do Limagem, Benguela province, rocks, 0-2 m, 1 spm.; Baia de Santa Maria, Benguela province, rocks 0-2 m, 3 spm., 1 v.; Baia da Lucira (Bissonga), Moçâmedes province, rocks at low tide, 1 spm.; Lucira (Praia do Cesar), Moçâmedes province, 3 spm.; Chapeu Armado, Moçâmedes province, rocks at low tide, 5 spm.; Praia Amelia, Moçâmedes province, rocks at low tide, 3 spm., all leg. GOFAS, 1982-85; all MNHN.

BIOTOPE : Byssally attached to rocks, stones, shells and other hard objects, from low tide about 40 m.

REMARKS

This species despite its variability should not be confused with other west African species of *Barbatia* as it is the only species with the distinctive well spaced concentric ridges which give the periostracum a frilled appearance. It is also the only species to be encountered in the rocky lower intertidal and sublittoral.

We investigated the possibility that as in the Indo-Pacific there might be two closely related species equivalent to *B. foliata* (Forsskål, 1775) and *B. decussata* (Sowerby, 1833). Despite the variability in form of the west African specimens we could find no indication of pattern except that crevice dwelling examples were usually fore shortened or distorted.

Barbatia complanata belongs to the group of species represented by *B. candida* (Helbling, 1779) in the Caribbean, by *B. foliata* (Forsskål, 1775) in the Indo-Pacific and by *B. reeveana* (d'Orbigny, 1846) in the Panamic province. The west African species differs in having a much finer sculpture with approximately twice as many anterior and median primary riblets and in the posterior riblets narrower, more regular and numbering from 6-7 rather than the 3-4 typical of the Caribbean species. The periostracum of *B. candida* is heavier and the emergent bristles are consequently much longer and more robust. The Indo-Pacific *B. foliata* is an altogether much larger species with a more coarse sculpture which lacks the regular, well spaced concentric ridges. The west African species is therefore closer to that of the Caribbean.

American authors place these species in the subgenus *Cucullearca* Conrad, 1865. These species are distinct from those of *Barbatia* sensu stricto such as *B. barbata* and *B. gabonensis* (see below) but we are not certain of the affinities with other, mainly Indo-Pacific, groups and refrain from using this taxon until a more thorough revision is completed.

Barbatia gabonensis n. sp.

(Pl. III, 6A-B; fig. 14; map 5)

TYPE MATERIAL : Holotype (27.7 mm), MNHN, off Mayumba, Gabon, 3°25′ S/9°56′ E, 100 m, trawled R/V "Thierry", Guinean Trawling Survey, Sta. 58/6, 30.XI.1963. Paratypes : NMWZ, Ilha de Luanda, Angola, 90 m, 1 spm., leg. GOFAS; MNHN, off Grand Bassam, Côte d'Ivoire, 5°00′ N/3°23′ W 100 m, 1 spm., trawled R/V "La Rafale", Guinean Trawling Survey, Sta. 26/6.

TYPE LOCALITY : Mayumba, Gabon.

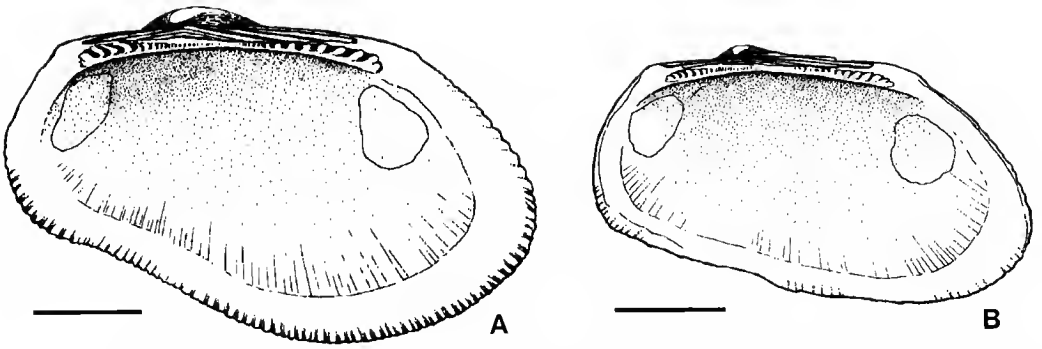


FIG. 12. — Internal views of right valves of *Barbatia complanata* (Bruguière) : A, Côte d'Ivoire; B, Angola. (Scale bar = 10 mm.)

DESCRIPTION

Shell to 30 mm in length, not very thick for the genus. Equivalve, not inflated. Inequilateral, beaks in the anterior quarter.

Outline roughly rectangular, longer than high, length : height ratio from 2.2-2.6 : 1, dorsal and ventral margins more or less parallel. Posterior area indistinct; posterior angle smoothly rounded; posterior margin oblique, gently curving to posterior ventral junction which is narrowly rounded or subacute. Median area flattened or weakly depressed; byssal gape very narrow, short; ventral margin gently curved to straight, byssal sinus if present, weak. Anterior margin in smaller shells broadly rounded; later becoming more straight, oblique with a narrowly rounded anterior ventral junction. Dorsal margin moderately long, more or less straight.

Dorsal area very narrow, cleft; umbonal separation slight. Ligament restricted to area between and behind the beaks, chevrons narrow, numbering up to 7.

Hinge plate moderately thick, teeth in two series which are barely separable but the junction lies below the beaks, anterior set up to 10 teeth, posterior set up to 16 teeth. Teeth serrated, straight or slightly chevron shaped, becoming a little oblique towards the margins of the plate.

Sculpture fine of nodulose radial riblets, 90-110 in number more or less uniform in size with the exception 13-18 pairs of larger riblets which border distinct radial grooves.

Periostracum mostly lamellar except for long, subtubular, semispathulate bristles arising from the radial grooves. Lamellae straw coloured, bristles dark brown.

Shell mostly white, some with faint tinges of brown or brownish pink colour.

Adductor scars subequal, the posterior a little longer, posterior pedal/byssal retractor long and very narrow.

SELECTED SHELL MEASUREMENTS

Length (mm)	Height (mm)	Tumidity (mm)	Anterior margin to beak (mm)	Rib No.	Groove No.
26.9	16.1	12.1	8.3	92	13
29.9	16.9	13.5	7.6	105	17
22.0	11.8	8.7	5,6	100	16
23.5	13.2	10.2	6.4	98	16
26.2	15.6	10.7	7.7	108	15
21.5	15.6	8.4	5.9	109	18

DISTRIBUTION : *Barbatia gabonensis* is an entirely tropical species with a restricted distribution from Liberia south to northern Angola.

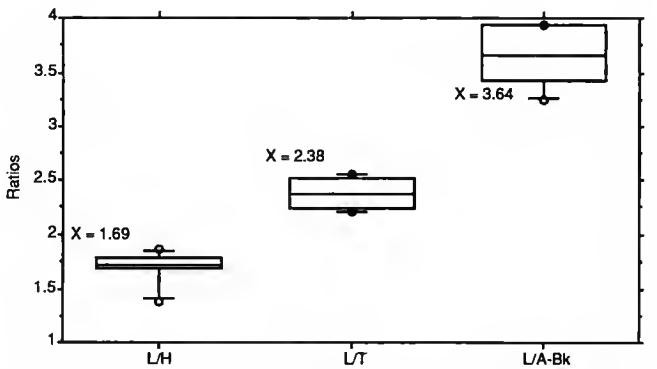


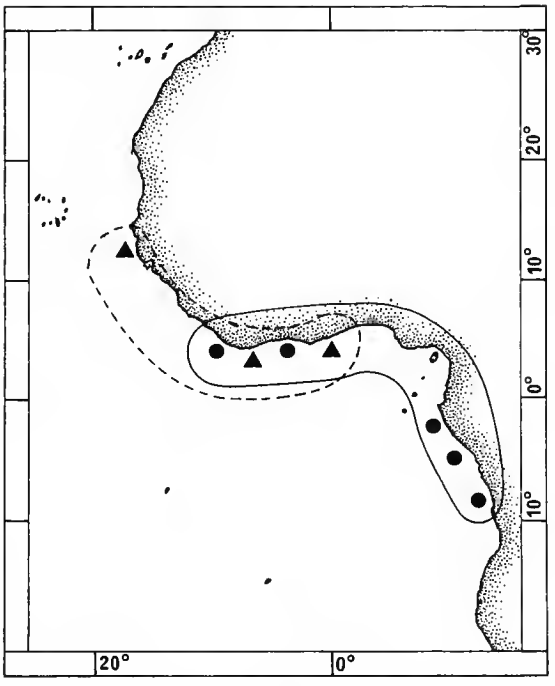
FIG. 13. — Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Barbatia gabonensis* from West Africa.

MATERIAL EXAMINED : The type material; **Liberia** : 4°37′ N/10°50′ W, 90-100 m, 2 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 24.V.1956, MNHN. **R.P. Congo** : off Pointe-Noire (no precise locality), 1 spm., leg. MARCHE-MARCHAD, MNHN.

BIOTOPE : *Barbatia gabonensis* is a deep water form with the present data indicating a range around 100 m. The byssus is functional although small and this suggests that this species lives attached to rock, stones or other hard substrates. The byssus is much weaker than in related forms from the littoral and sublittoral zones further suggesting that the local conditions are tranquil or sheltered. This could be explained by the lack of wave action at the depths from which *B. gabonensis* has been recovered.

DERIVATIO NOMINIS : *gabonensis* from Gabon, the country where the type locality is situated.

REMARKS : The immediate distinctive feature of this species is the series of radial grooves and the long periostracal bristles arising from them. This distinguishes it from the *Barbatia*



MAP 5. — Distribution of *Barbatia gabonensis* (circles) and *B. ionthados* (triangles).

candida-complanata-foliata complex in which the bristles are not differentiated. Some species have differentiated bristles but none so marked or in such widely separated rows as *B. gabonensis*. *Barbatia sculpturata* Turton, 1932 is also much smaller and has only a few broad ribs on the posterior area, it is restricted to the sublittoral zone of the coasts of Natal and Cape Province (S. Africa) (KILBURN, 1983). *Barbatia barbata* (Linné, 1758) from the Mediterranean has a similar bristle pattern when small but later there is much less distinction between the primary and secondary bristles and in the largest specimens the whole of the dorsal area is thatched. Furthermore in *B. barbata* the ligament fills the whole of the dorsal area. *Barbatia pistacia* (Lamarck, 1819) from south eastern Australia has a similar rib pattern but the bristles are poorly differentiated and the rows of larger bristles are much more numerous.

Barbatia ionthados n. sp.

(Pl. III, 7A-B; fig. 15; map 5)

TYPE MATERIAL : Holotype (20.6 mm), MNHN, South of Bassam, Côte d'Ivoire, 200 m, leg. MARCHE-MARCHAD, 13.X.1960. Paratypes : MNHN, off Cape three Points, Ghana, 4°43,5′ N/2°45,5′ W, 100 m, 1 spm., trawled R/V "La Rafale", Guinean Trawling Survey II, Sta. 27/6, 20.III.1964; NMWZ, as previous, 1 spm.

TYPE LOCALITY : South of Bassam, Côte d'Ivoire.

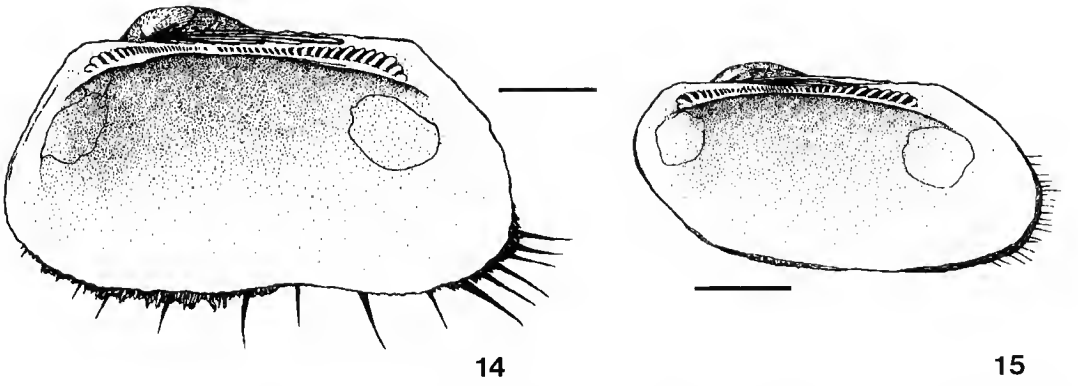


FIG. 14-15. — 14 : Internal view of right valve of *Barbatia gabonensis* n. sp. Gabon. 15 : Internal view of right valve of *Barbatia ionthados* n. sp. Côte d'Ivoire. (Scales bars = 5 mm.)

DESCRIPTION

Shell to 21 mm in length, very fragile. Equivalve. A little compressed. Very inequilateral, beaks in the anterior fifth.

Outline elongate rectangular, length to height ratio 2.6-2.7 : 1, dorsal and ventral margins more or less parallel. Posterior area not expanded but rather long, posterior angle rounded but distinct, posterior margin oblique to broadly rounded, posterior ventral junction rounded. Median area lacking sinus, ventral margin more or less straight, byssal gape minute. Anterior margin broadly rounded. Dorsal margin long, more or less straight.

Dorsal area very narrow, slightly cleft, umbonal separation slight. Ligament situated entirely behind the beaks, chevrons narrow numbering up to 4.

Hinge plate long, narrow; teeth in two series, separated by a very small gap at a point below the beaks; anterior set up to 9 teeth, posterior set up to 31 teeth. Teeth small, more or less straight, finely serrated; central teeth more or less vertical, lateral teeth slightly oblique.

Sculpture very fine, of weakly nodulose radial riblets, 88-96 in number but those on the anterior margin are difficult to distinguish and some shells may have more riblets. The riblets show no pattern except that they become progressively finer towards the anterior.

Periostracum of long very fine dark straw coloured suberect bristles which are longest on the posterior angle and most erect on the posterior slope. There is no trace of inter bristle lamellae.

Shell uniformly white.

Inner margin weakly serrate corresponding to radial riblets. Adductor scars subequal, posterior pedal/byssus retractor narrowly elongate. Byssus a thin narrow strap.

SELECTED SHELL MEASUREMENTS

Length (mm)	Height (mm)	Tumidity (mm)	Anterior margin to beak (mm)	Rib No.
20.6	9.7	7.5	4.0	88
19.1	9.3	7.3	3.8	96
11.1	5.6	4.2	2.1	90

DISTRIBUTION : Living specimens have been taken only off the northern coast of the Gulf of Guinea. A number of worn valves from off Senegal suggests a wider distribution and one might expect this species to occur throughout tropical West Africa.

MATERIAL EXAMINED : The type material; **Senegal** : off Gorée, 80 m, 8 v., poorly preserved, dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 20.II.1956, MNHN.

BIOTOPE : From the limited material available *B. ionthados* is apparently a deep water species living from 100-200 m. The functional byssus and general shell form suggest that it is epibyssate living attached to hard substrates. As with its Indo-Pacific counterpart *Barbatia tenella* Reeve, 1844 it may live in crevices or under stones where there is shelter but in the deep waters preferred by *B. ionthados* such protection may not be required.

DERIVATIO NOMINIS : *ionthados*, Greek, "long haired" or "shaggy", referring to the form of the periostracum.

REMARKS : Only one other species resembles *B. ionthados*, that is *B. tenella* Reeve, from the Indo-Pacific which shares the fragile shell, posterior ligament, fine sculpture and an entirely spicate periostracum. DALL, BARTSCH and REHDER (1938) erected the genus *Barbarca* and IREDALE (1939) the genus *Opularca*, for species close to this form. As they are clearly linked to *Barbatia* they would only warrant subgeneric status of which the earliest name is *Barbarca*.

Barbatia legumen (Lamy, 1907)

(Pl. III, 8, 9A-B, 10; fig. 16-18; map 6)

Arca legumen Lamy, 1907 : 74-76, pl. 1, fig. 3-4.

TYPE MATERIAL : MNHN, 16 syntypes from three different localities : 5 spm. Gabon, coll. DIBOWSKY, 1893; 5 spm., no locality, coll. LARGENTIÈRE, 1887; 2 spm., 4 v., "Bata Congo" (= Bata in Equatorial Guinea), coll. POBEGUIN, 1891. Among the latter lot is the specimen figured by LAMY (1907) and this is here selected as the lectotype.

TYPE LOCALITY : Bata, Equatorial Guinea. On the original label of the POBEGUIN collection this locality is always cited as "Bata Congo", at that time it belonged to the French Congo and did not become Spanish until 1900.

DESCRIPTION

Shell to 52 mm in length. Equivalve. Compressed. Inequilateral, beaks in the anterior third.

Outline of adult submytiliform, often arcuate, anterior part narrow, posterior part expanded. Posterior area small; posterior angle broad, rounded and forming greater part of the posterior half of the shell; posterior margin long, oblique, sloping steeply, dorsal auricule indistinct or lacking. Median area distinctly sinuate, ventral margin long, arcuate. Anterior area small, demarcated by a rounded anterior angle; anterior margin narrowly rounded. Dorsal margin moderately long, straight. Outline of juveniles similar but posterior margin shorter and distinctly auriculate, ventral margin less arcuate and anterior area larger but anterior angle indistinct. The increasing arcuate development with age is illustrated in figure 17.

Dorsal area very narrow, deeply cleft; umbonal separation slight, ligament barely visible in joined valves. Ligament filling the whole of the dorsal area including the anterior part; ligament almost entirely lamellar, chevrons very strong numbering up to 5.

Hinge plate moderately thick; teeth probably in two series but the central teeth are usually worn giving the appearance of distinct anterior and posterior sets. When well preserved up to 50 teeth in all. Teeth slightly chevron shaped, finely serrated, becoming oblique laterally.

Sculpture of very numerous radial riblets, usually worn but best preserved in median sinus.

Periostracum initially with broad appressed bristles on posterior angle but later consisting primarily of thick concentric lamellar layers with scarcely emergent bristles. Colour a deep tanned dark brown.

Shell external colour white to cream, internally bluish in juveniles white in adults.

Adductor muscle scars unequal, the posterior twice the size of the anterior. Posterior pedal/byssus retractor small, narrowly oval.

SELECTED SHELL MEASUREMENTS : See figure 16.

DISTRIBUTION : *Barbatia legumen* occurs only in the southern part of tropical West Africa, from Equatorial Guinea to southern Angola (Santo Antonio). The greater part of this range lies within the influence of the cold Benguela Current which in the southern winter can reach the coast of Gabon. Here and in Equatorial Guinea it seems to be very rare.

MATERIAL EXAMINED : The type material; **R.P. Congo** : Pointe Indienne, rocky shore 1 sh.; Pointe-Noire, Plage Sauvage, on beach, 3 v.; Plage Mondaine, on beach, numerous sh. and v.; off Plage ORSTOM, 3-7 m, numerous sh. and v., all leg. VON COSEL, XI-XII.1985; several sh. and v., leg. CROSNIER (Office Pte.-Noire); all MNHN. **Angola** : 10 km S of Ambrizete, Zaire province, intertidal, on beach, many fresh sh. and v.; Barra do Dande, Bengo province, between rocks at low tide, 2 spm.; Baia São Tiago, Bengo province, between rocks at low tide, 4 spm.; Cacuaco, Bengo province, between rocks, 0-1 m, 14 spm.; Corimba, Luanda province, Praia Etambar, between rocks at low tide, 5 spm., 1 sh. ; Cabo Ledo, Luanda province, 10 m, 11 juv. spm., 3 juv. sh.; Santo Antonio, Benguela province, between rocks at low tide, 1 spm.; Baia das Pipas, Moçâmedes province, on rock platform, 1 juv. spm.; Porto Alexandre, Moçâmedes province, 2 m, 1 juv. v., all leg. GOFAS, 1982-85; all MNHN.

BIOTOPE : This species lives byssally attached to rocks, on the undersides of stones and to secondary hard substrates on soft sediments. The bathymetric range is from the intertidal to 1-2 m in the sublittoral.

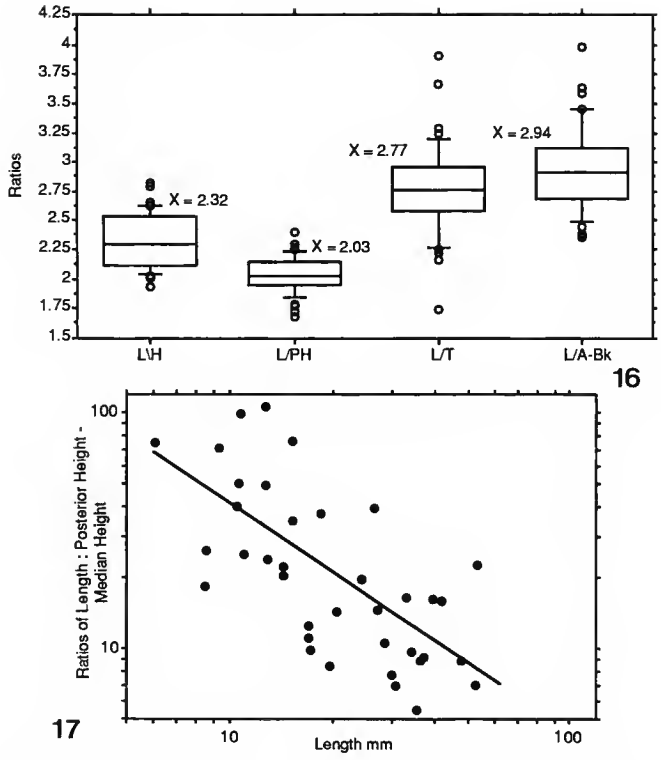


FIG. 16-17. — 16 : Box plots of the ratios of Total Shell Length to Height (L/H), Posterior Height (L/PH), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Barbatia legumen* from West Africa. 17 : Graph of the ratio Total Shell Length : Difference in Median and Anterior Height plotted against Total Shell Length on log axis, showing the increasing arcuate form of the shell with age in *Barbatia legumen*.

REMARKS

Barbatia legumen belongs to a group of species which are submytiliform in shape and are typical inhabitants of the littoral and shallow sublittoral throughout the Indo-Pacific. The most widespread of these related species are *B. obliquata* (Gray, 1837) [Indian Ocean] and *B. virescens* (Reeve, 1844) [Indo-West Pacific]. *B. obliquata* is more expanded posteriorly, not auriculate and the ligament is restricted to behind the beaks. *B. virescens* can be auriculate and the ligament is on both sides of the beaks but the outline is much shorter, the sculpture more pronounced and the periostracum more spicate.

Some submytiliform species have been given generic rank ; *Savignyarca* Jousseaume, 1898 (type *S. savignyarca* = *Barbatia obliquata*) ; *Obliquarca* Sacco, 1898 (type, *Arca modiliformis* Deshayes, 1831) and *Barbatirus* Iredale, 1939 (type *B. minulus* Iredale, 1939). HABE (1977) regards these as synonyms of *Savignyarca* but this presupposes that the submytiliform species have a common ancestry. We do not regard the common adaptive form as sufficient evidence to conclude monophyly because the incidence of convergent radiations within the Arcoidea is

well documented (STANLEY, 1972). In recent forms the convergent radiations within the Arcidae and Noetiidae illustrate the point.

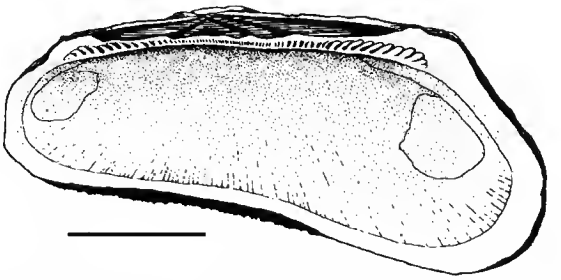


FIG. 18. — Internal view of right valve of *Barbatia legumen* Lamy. Angola. (Scale bar = 10 mm.)

Subgenus **NIPPONARCA** Habe, 1951

It has not been our intention to introduce subgenera within *Barbatia* but in this case we have both anatomical and shell characters which allow us to confirm that *Nipponarca* is a useful division.

TYPE SPECIES : *Arca bistrigata* Dunker, 1858 : 87, pl. 30, fig. 4, see also HABE, 1951, fig. 49.

REVISED DIAGNOSIS : Shells to 50 mm. Equivalve. A little compressed. Inequilateral, beaks in the anterior third. Outline subrectangular, distinctly longer than high, dorsal and ventral margins subparallel. Hinge plate long, straight, teeth small. Dorsal area flat or almost so. Sculpture of few radial ribs; posterior ribs rather broad, flat and weakly sculptured; median ribs bifurcate, nodulose. Periostracum with long semi-erect bristles arising from the interspaces of the posterior angle. Labial palps very large with numerous sorting ridges. Byssate species inhabiting inshore areas where the conditions are turbid and often under estuarine influences.

SPECIES INCLUDED : *Barbatia* (*Nipponarca*) *bistrigata* (Dunker, 1858) [Indo-Pacific, Pakistan to Japan]. *Barbatia* (*Nipponarca*) *allocostata* this paper [tropical west Africa, Senegal to Sierra Leone]. Probably *Barbatia signata* (Dunker, 1858) [Indo-Pacific, India to China].

Barbatia (Nipponarca) allocostata n. sp.
(Pl. IV, 1A-B, 2; fig. 19, 20; map 6)

TYPE MATERIAL : Holotype (28.4 mm), MNHN, Mouth of Rio Geba, Guinea-Bissau, 11°57,5′ N/16°27′ W, 7 m, agglomerations of live and dead *Crassostrea gasar*, on oyster shells, trawled R/V "André Nizery", leg. VON COSEL, 9.X.1988. Paratypes as holotype; MNHN, 9 spm.; NMWZ, 1990.017, 5 spm.

TYPE LOCALITY : Mouth of Rio Geba, 11°57,5′ N/16°27′W, Guinea-Bissau.

DESCRIPTION

Shell to 35 mm in length. Equivalve. A little compressed, most inflated across the anterior umbonal region and narrowing posteriorly. Inequilateral, beaks in the anterior third.

Outline subrectangular, much longer than high. Posterior area long, weakly demarcated, posterior angle rounded and becoming obsolete; posterior margin initially rounded, more or less vertical becoming oblique and some auriculate; posterior ventral junction rounded. Median area sulcate, ventral margin more or less straight, usually indented at byssal gape which is relatively short and narrow. Anterior area short, demarcated by weak anterior ridge; anterior margin broadly rounded. Dorsal margin long, straight.

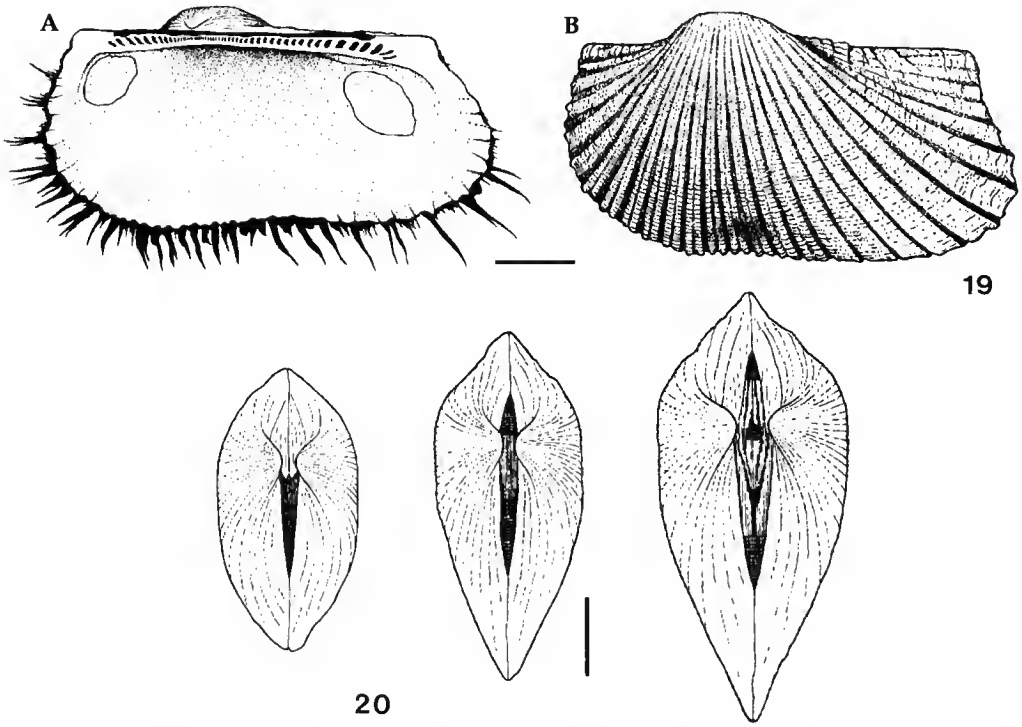


FIG. 19-20. — 19 : *Barbatia* (*Nipponarca*) *allocostata* n. sp. A, internal view of right valve; B, external view of left valve with periostracum removed. Guinea-Bissau. 20 : Size series of dorsal views of *Barbatia* (*Nipponarca*) *allocostata* n. sp. Guinea-Bissau. (Scales bars = 5 mm.)

Dorsal area narrow, weakly cleft to flat, umbos well separated. Ligament initially behind the beaks but developing anteriorly in larger specimens; chevrons few, numbering up to 3.

Hinge plate narrow, teeth in two series but separation is indistinct, total number 50. Teeth small, weakly serrated, more or less straight, vertical centrally becoming a little oblique laterally.

Sculpture of relatively few, 26-28, radial ribs. Posterior 10-12 ribs broad, flat, more or less smooth; median ribs deeply bifurcate, nodulose; anterior ribs simple, irregularly nodulose.

Periostracum of very long semierect bristles arising from the rib interspaces over the posterior angle, elsewhere the pattern is the same but the bristles are much shorter and fragile. Bristles dark brown, remainder paler.

Shell mostly white but externally umbos grey and some with brown blotches on the posterior area; internally the umbonal cavity is suffused with green or greyish green tints.

Adductor muscle scars unequal, the posterior half as big again as anterior scar. Posterior pedal/byssus retractor scar narrowly elongate.

Anatomy (the following account is based on preserved specimens only)

The mantle edge (fig. 21) is entirely unfused and thickened posteriorly where it is thrown into small folds. Pigmentation is weak with only a few brown patches on the exterior of the outer fold in the posterior ventral region. Eyespots are absent but there is a single anterior dorsal pigment spot.

The gills (fig. 21) are typically arcoid and the gill axis is contorted suggesting that it is muscular and capable of extending the gills to the margin of the shell. The labial palps (fig. 21) are very large, semicircular in outline and with about 90 sorting ridges. These palps are very large for the genus, most being narrow with about 15-20 ridges.

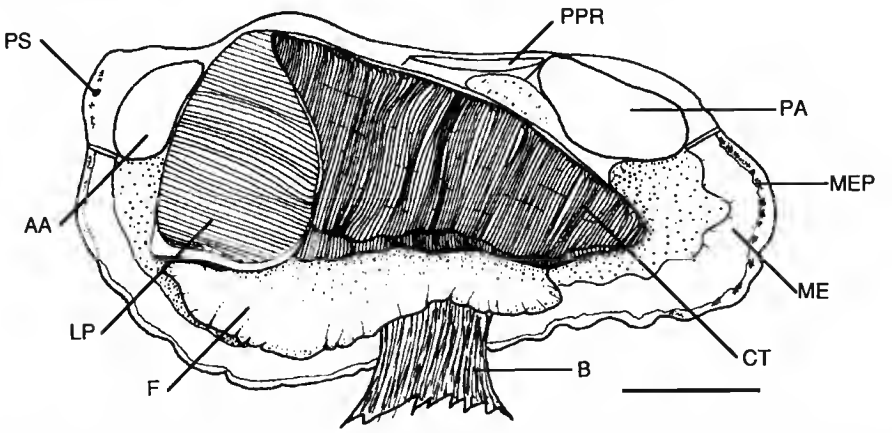


FIG. 21. — Gross anatomy of *Barbatia* (*Nipponarca*) *allocostata* n. sp. viewed from the left side after removal of the left valve and mantle. (Scale bar = 5 mm.)
AA, anterior adductor muscle; B, byssus; CT, ctenidium; F, foot; LP, labial palps; ME, folded mantle edge; MEP, mantle edge pigmentation; PA, posterior adductor muscle; PPR, posterior pedal retractor muscle.

The gut is typical of the genus with a short oesophagus entering the stomach on its anterior dorsal face; the mid gut exits from the ventral floor of the stomach and passes deeply into the foot where it is weakly folded before forming a large anterior loop, then it passes dorsally across the right hand side of the stomach before bending posteriorly as the hind gut. The anterior loop is more prominent than in other species of *Barbatia*. The stomach is typically arcoid but the food sorting area is restricted to the anterior dorsal food sorting caecum which is endowed with prominent sorting ridges. The right and anterior ventral

embayments have openings to the digestive diverticula and ridges are restricted to the rejection tract which follows the major typhlosole.

The foot (fig. 21) is large with a well developed heel and toe. The byssus groove is centrally placed and produces a relatively large but narrow sheet byssus (fig. 21) typical of the genus. The size of the byssus is reflected in the large posterior pedal/byssus retractor muscles which are narrowly elongate in section.

The anatomy of this species is similar in most ways to that of *Barbatia* as a whole in that it reflects an epibyssate habit. Significantly different is the size of the labial palps which are more typical of infaunal forms such as some *Anadara* species (HEATH, 1941 and LIM, 1966) and a new genus to be described in Part two of this revision. The biotope described below does appear to be one where resuspended matter is dense and this would explain the adaptive value of this epibyssate species having a large sorting capacity. A little surprisingly are the apparently weak mantle edge folds, these are usually more developed in species which inhabit muddy biotopes. The lack of pigmentation and eyespots on the mantle edge are not characteristics of *Barbatia* but again can be explained if the water column is so full of suspended matter that light is virtually excluded.

SELECTED SHELL MEASUREMENTS : See figure 22.

DISTRIBUTION : This species seems to have a limited distribution to the northern part of tropical West Africa. It is actually known from the extreme south of Senegal (southern Casamance) to the border between Guinea and Sierra Leone. Most probably it goes further south into Sierra Leone but we have never seen material from south of 9° N.

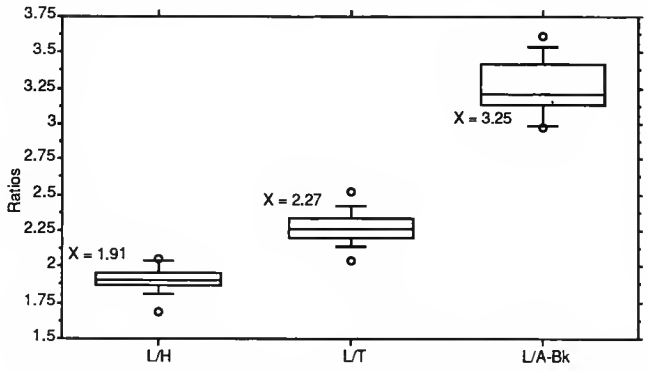
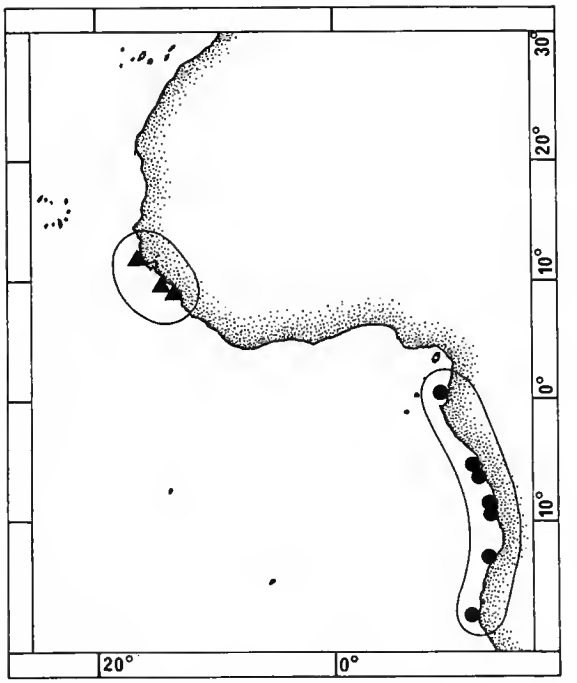


FIG. 22. — Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Barbatia* (*Nipponarca*) *allocostata* from West Africa.

MATERIAL EXAMINED : The type material; **Senegal** : Karabane Bôlon, Casamance, off Karabane, 4 m, 7 v.; Casamance, creek off Elinkine, 3 m. 3 v.; Ourong Bôlon, S-Casamance, 2-4 m, 2 v.; Cap Skirring-Diembéring, on beach, 1 v.; Essoukoudiak Bôlon, on the frontier to Guinea-Bissau, 4-6 m, coarse sand with pebbles, 1 spm., many v., all leg. VON COSEL, 5-17.III.1988, all MNHN. **Guinea-Bissau** : Mouth of Rio Geba, 11°57,5′ N/16°27′ W, 7 m, on oysters (from type lot), 48 associated spm., MNHN. **Guinea** : Kaporo, NW coast of Conakry Peninsula, in front of ORSTOM, low tide, undersides of rocks, 1 spm.; Kaporo Port, Conakry Peninsula, rocks at low tide, 1 v.; Dixinn Port, NW coast of Conakry Peninsula, gravel, low tide, 1 v.; Conakry, Corniche Sud, in front of the "People's Palace", rocks at low tide, 4 v.; Kassa, Iles de Los, E-side, N of village, on the underside of a stone at low tide, 1 spm., all leg. VON COSEL, V and XI.1988, all MNHN.



MAP 6. — Distribution of *Barbatia legumen* (circles) and *B. allocostata* (triangles).

BIOTOPE : *Barbatia* (*Nipponarca*) *allocostata* occurs on hard bottoms such as stones and rocks and is byssally attached. It is frequently found on offshore oyster beds consisting of *Crassostrea gasar* (Dautzenberg, 1891) where it is attached in crevices and between oyster shells. In Guinea-Bissau it was taken in trawls from sandy bottoms where it was found on shells of living *Cymbium pepo* (Lightfoot, 1786) which were also covered by small oysters. It was likewise found on living or hermit crab inhabited shells of *Pugilina morio* (L., 1858) and even on oyster covered valves of large bivalves like *Macoma cancellata* (Sowerby, 1873) and *Mactra rostrata* Spengler, 1802. *B. allocostata* seems to be limited to murky, sediment and seston laden water in regions with estuarine influences and seasonal salinity changes. On the rocky shores of the Conakry peninsula it was found on the sides and undersides of stones at low tide and is a rare but regular member of the *Crassostrea gasar* community. *B. allocostata* is not common in the intertidal and is most frequently found offshore to about 15 m.

DERIVATIO NOMINIS : *allocostata*, Greek, compounded from *allasso* meaning "to change" and *costatus* meaning "to bear ribs". This refers to the abrupt change in the form of the radial ribs from the median to posterior areas.

REMARKS : *Barbatia* (*Nipponarca*) *allocostata* is very closely allied to *B.* (*N.*) *bistrigata* (Dunker, 1858). The latter species is heavier shelled, reaches a larger size, the marginal crenulations are stronger, the anterior most, posterior ribs develop up to 4 ridges which do not bisect the rib and the posterior angle periostracal bristles are shorter and more stout.

Genus **BENTHARCA** Thiele, 1931

TYPE SPECIES : *Arca nodulosa* Müller, 1776.

Bentharca asperula (Dall, 1881)
(Pl. VIII, 6A-B; fig. 23)

Macrodon asperula Dall, 1881 : 120-121.
Arca profundicola Verril & Smith *in* VERRILL, 1885 : 439-440, pl. 44, fig. 23-23a.
Arca (*Barbatia*) *pteroessa* Smith, 1885 : 844.

TYPE MATERIAL : In USNM.

TYPE LOCALITY : Off S. E. United States, "Blake" sta. 33, 2875 m.

DESCRIPTION

Shell to 12 mm in length. Equivalve. Somewhat compressed. Inequilateral, beaks in the anterior quarter.

Outline subtrapezoidal. Anterior area greatly restricted, posterior roundly expanded giving an overall wedge-shaped appearance. Posterior margin broadly rounded; ventral margin sloping to narrow anterior margin, the latter slightly indented by byssal sinus. Median byssal sinus present at all sizes but byssal gape indistinct. Dorsal margin long and straight.

Dorsal area long, narrow initially but expanding rapidly with age. Ligament restricted to the posterior area but filling area between beaks with maturity.

Hinge plate very narrow; teeth in two series, separated by a wide edentulous gap. Teeth numbering up to five in each set; posterior teeth becoming subparallel to dorsal margin.

Sculpture very weak, of faint radial striae only. In other regions the sculpture can be a little stronger with faint raised riblets.

Periostracum usually worn and preserved at margins only; of very slender appressed bristles.

Colour white, periostracum a dirty olive brown.

Adductor muscle scars indistinct but unequal, the posterior about twice the size of the anterior. Byssus retractor muscle small, reflecting the weak byssus which consists of a single narrow strap.

DISTRIBUTION : A cosmopolitan species restricted to the abyssal zone from 2000-5000 m.

MATERIAL EXAMINED : Based on the data in OLIVER and ALLEN (1980).

BIOTOPE : *Bentharca asperula* lives attached to small stones, gravel and grit particles.

REMARKS : Two species of *Bentharca* occur in the Atlantic Ocean but the second *B. nodulosa* (Müller, 1776) has not yet been recorded from tropical West Africa. *B. nodulosa* lives

at shallow depths in the subarctic region and undergoes increasing submersion towards the south of its range reaching 3000 m off Madeira. It is a larger shell with a more coarse sculpture resembling that of the genus *Acar*.

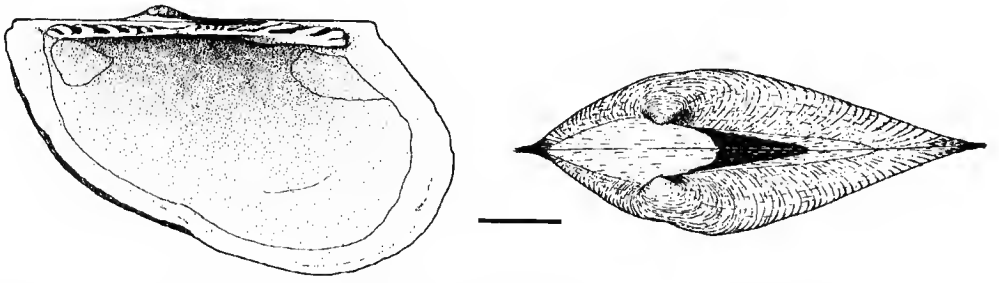


FIG. 23. — Internal view of right valve and dorsal view of *Bentharca asperula* (Dall). Angola, 3975 m. (Scale bar = 2 mm.)

Subfamily ANADARINAE

Genus **ANADARA** Gray, 1847

TYPE SPECIES : *Arca antiquata* Linné, 1758 (OD).

DIAGNOSIS : The generic systematics of most of the Anadarinae is presently confusing, especially concerning the distinction between *Anadara, Scapharca* and *Cunearca*. The distinctions as detailed by NEWELL in MOORE (1969) rest on the form of the ligament and on the equality of size of right and left valves. The ligament is referred to as amphidetic or opisthodetic, however in many species the ligament initially develops behind the beaks and eventually grows to fill the whole of the dorsal area. The degree of overlap of the right valve also has an ontogenetic relationship as well as being variable between species of obvious similarity in general form. These characters therefore are unreliable when used in isolation and NEWELL's definitions are consequently too broad. Other genera and subgenera have been revived or introduced mainly by OLSSON (1961) for panamic forms and by IREDALE (1939) for Australian forms. OLSSON (1961) uses a wider range of characters yet there is still reliance on some that do have ontogenetic changes and he does not compare his subgenera with those from the Indo-Pacific. Consequently a few divisions appear to be stable such as *Rasia* Gray, 1857; *Larkinia* Reinhart, 1935 and *Caloosarca* Olsson, 1961. In other cases such as OLSSON's (1961) use of *Diluvarca* Woodring, 1925 there remains a wide interpretation with some overlap into *Anadara* and *Scapharca* forms.

Our conclusion is to use *Anadara* as a broad generic group with subgeneric designations reserved for those cases where there is a clear resemblance in overall form to the type species of the subgenus concerned. There is clearly the need for a revised generic systematics on a world wide scale but this is beyond the scope of this paper and we refrain from introducing revised concepts in isolation.

Anadara geissei (Dunker, 1891)
(Pl. IV, 3A-B, 4A-B, 5, 6A-B; fig. 24; map 7)

Arca setigera Dunker, 1853 : 45, pl. 9, figs. 16-18 (non Reeve, 1844).
Arca (*Anomalocardia*) *dunkeri* Kobelt, 1891 : 162, pl. 41, figs. 2-4.
Arca (*Anomalocardia*) *geissei* Dunker in Kobelt, 1891 : 163-164, pl. 41, figs. 5-6.

Type material : In SMF Frankfurt.

Type locality : Senegal.

Description

Shell to 75 mm in length. Slightly inequivalve in juveniles but adults more or less equivalve. Not inflated, tumidity approximately 1/2 to 1/3 of the length. Inequilateral, beaks in the anterior third.

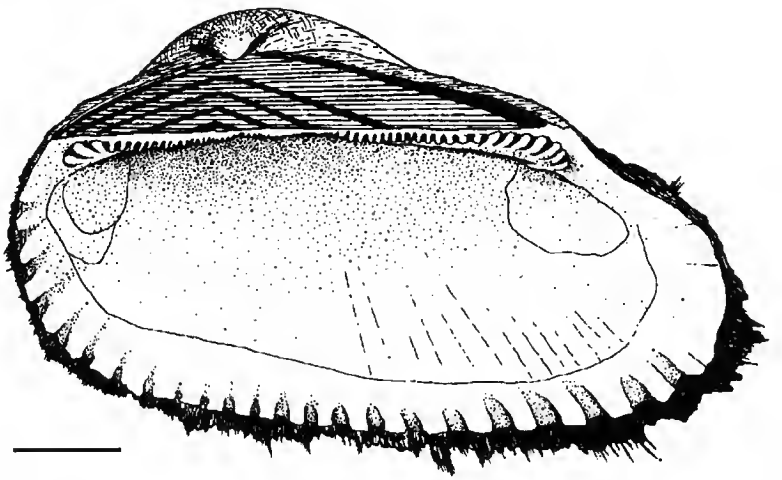


Fig. 24. — Internal view of right valve of *Anadara geissei* (Dunker). Angola. (Scale bar = 10 mm.)

Outline oblong, subrectangular, distinctly longer than high, juveniles distinctly expanded posteriorly, adults symmetrical. Posterior area indistinct; posterior angle marked in juveniles but becoming obsolete early in ontogeny; posterior margin obliquely subtruncate and slightly auriculate in juveniles, becoming simply subtruncate and finally rounded but more acute than anterior margin. Median area initially weakly sulcate, this noticeable to about 30 mm, then becoming progressively obsolete; ventral margin rather long and more or less straight, larger examples with a narrow anterior ventral byssus gape. Anterior margin broadly rounded. Dorsal margin rather long, straight.

Dorsal area long, rather narrow except in the largest specimens, umbonal separation moderate. Ligament initially opisthodetic but developing anteriorly at about 6 mm, apparently amphidetic by 15 mm and remaining with a single lateral chevron bordering a large fibrous sheet until about 40 mm when new chevrons are added these totalling 4-5 in the largest specimens.

Hinge plate rather narrow to moderate depending on the degree of encroachment by the ligament; teeth in two series, separation distinct, anterior set up to 30 teeth, posterior set up to 35 teeth. Teeth small, median series more or less straight and vertical; lateral series slightly chevron shaped, slightly oblique.

Sculpture of 29-32 radial ribs of which up to 18 anteriorly become progressively bifurcate, posterior ribs wider and more flat, anterior ribs very weakly ridged by low closely spaced cross bars.

Periostracum a thick coating of appressed laminae with bristles developing from the primary interspaces and from the bifurcate interspaces; anterior and median bristles short, lanceolate and soft, posterior bristles coarse, long, rigid, semi-erect; colour a deep reddish brown except for posterior bristles which are black; juveniles have a distinctive maculate pattern over the posterior area formed by differential thickening of the periostracum.

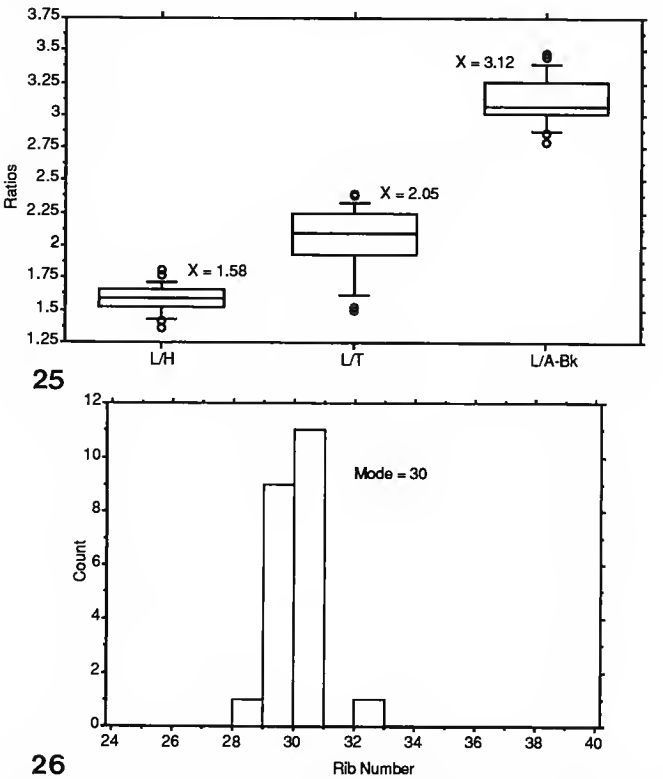


FIG. 25-26. — 25 : Box plots of the ratios of Total Shell Length to Heigth (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Anadara geissei* from West Africa (n = 27). 26 : Bar chart of Rib Number for 22 shells of *Anadara geissei*.

Shell white.

Adductor scars subequal, the posterior a little larger; posterior pedal/byssal retractor elongate oval. Inner margin deeply crenulate.

SELECTED SHELL MEASUREMENTS : See figure 25.

DISTRIBUTION : This species ranges from the Cape Verde Islands and Mauritania (Cap Blanc) to southern Angola (Benguela).

MATERIAL EXAMINED : **Mauritania** : Off Port Étienne, 20°20′ N/16°22′ W, 10 m, 3 v., coll. MARCHE-MARCHAD, 8.V.1965, MNHN. **Cape Verde Islands** : Sta. Lucia, 52 m, 1 spm. + 1 v., dredged R/V "Princess Alice" (sta. 1152), coll. H. FISCHER, 1901; off Boa Vista, 15 m, 1 spm., dredged R/V "Calypso", 1959; SW of Boa Vista, 30 m, 2 v., 23.X.1948; São Vicente, Baia Porto Grande, beach, 11 v., leg. VON COSEL, 19.XII.1978; São Vicente, Mindelo, beach, 3 v., leg. VON COSEL, 17.XII.1978; all MNHN. **Senegal** : No precise locality, 1 spm., coll. VAYSSIÈRE; Rufisque, 18-20 m, many spm.; Pte. Cansado, 2 v.; W of Cap Rouge, 6 v., all coll. Mission GRUVEL, IV.1909; Gorée, 1 spm., coll. BAVAY; Gorée, 1 spm., coll. GERET; Cap Vert, 1 v., coll. MAURY; off Dakar, 50 m, 4 v.; Banc de Seminole, 43-45 m, 1 v.; off Gorée, 95-98 m, many v., all dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 1954-1956; Dakar, Anse Bernard, 1 spm., leg. MARCHE-MARCHAD; SE of Gorée, 14°41′ N/17°23,2′ W, 17 m, fine sand and mud, many v., dredged R/V "Louis Sauger", leg. VON COSEL, III.1988; M'Bour, Petite Côte, on beach, 1 v., leg. VON COSEL, 22.III.1988; S. Casamance, Essoukoudiak Bôlon, 4-6 m, shelly sand, 1 v.; Karabane Bôlon, 3-4 m, shelly sand, 1 v., both leg. VON COSEL, III.1988; N. Casamance, Abéné, 13°03′N/17°03′ W, 20 m, very fine sand, 1 v.; Kafountine, 12°57,5′ N/17°16,8′ W, 35 m, medium sand and rocks, 1 v.; 12°56,9′ N/17°06,8′ W, 22 m, fine sand, 3 v.; 12°44,5′N/17°27,3′ W, 40 m, fine sand, 8 v.; 12°32′ N/17°28,8′ W, 45 m, fine sand, 3 v.; off Diembéring, 12°29,6′ N/17°24,3′ W, 35 m, fine sand, 1 v., all dredged R/V "Louis Sauger", leg. VON COSEL, III.1988, all MNHN. **Guinea-Bissau** : Ilhas Bissagos, 7 v., leg. Mission GAIN, 1913, MNHN. **Guinea** : 10°30′ N/15°43,5′ W, 21 m, 2 v.; 10°12′ N/13°06′ W, 20 m, 2 spm.; 9°50′ N/14°14′W, 15 m, 2 spm. + 5 v.; 9°30′ N/13°53′W, 19 m, 1 spm.; 9°18′ N/13°45′ W, 21 m, 1 spm.; 9°12′ N/14°15,1′ W, 33 m, 1 spm.; 9°05,7′ N/13°38′ W, 24 m, 1 spm.; all dredged R/V "André Nizery", leg. VON COSEL, IV-V.1988; 9°25′ N/13°48,5′ W, 1 v., dredged R/V "Président Théodore Tissier"; all MNHN. **Sierra Leone** : 7°15,5′ N/12°51′ W, 64 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 19.V.1956, MNHN. **Nigeria** : 4°00′ N/6°11′ E, 34 m, 3 spm.; 4°03′ N/6°12′ E, 32 m, many v., both dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, both MNHN. **Gabon** : 0°14′ S/9°14′ E, 15-16 m, 2 v., dredged R/V "Thierry", Guinean Trawling Survey, leg. CHERBONNIER, 16.XI.1963, MNHN. **R.P. Congo** : Pointe-Noire, off plage ORSTOM, 3-7 m, 1 spm., 1 v.; plage ORSTOM, on beach, 1 v., plage Mondaine, on beach, 6 v., all leg. VON COSEL, XI-XII.1985; all MNHN. **Angola** : Baia de Corimba, Luanda province, 10-20 m, many spm.; Cacuaco, Bengo province, 5-10 m, many spm.; Ponta das Lagostas, 5-20 m, 1 spm.; Santo Antonio, Benguela province, intertidal, 1 v., all leg. GOFAS, 1981-85, all MNHN.

BIOTOPE : *Anadara geissei* inhabits fine and mixed sand with calcareous algae and shell debris. The juveniles are byssally attached to hard objects. It is a subtidal species ranging from 3-30 m.

REMARKS

This species was first described by DUNKER in 1853 as *Arca setigera* but that name is preoccupied by *Arca setigera* Reeve, 1844. KOBELT (1891 : 162) renamed this *A. dunkeri* but he also then described (1891 : 163-164) *A. geissei* using a manuscript name from DUNKER. The two are undoubtedly synonymous, *A. geissei* representing a young specimen and *A. dunkeri* an adult, but as the name *A. geissei* has been applied in all previous regional faunal studies we have retained this name.

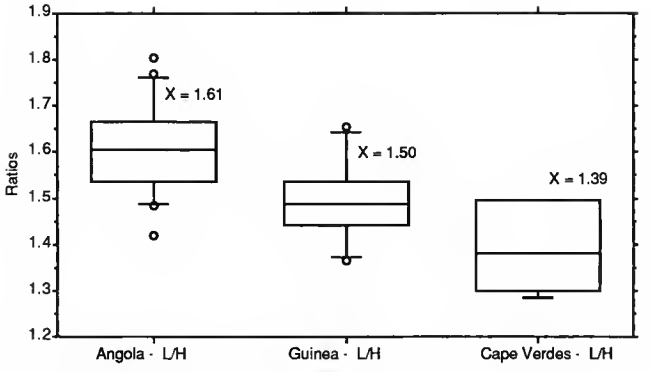
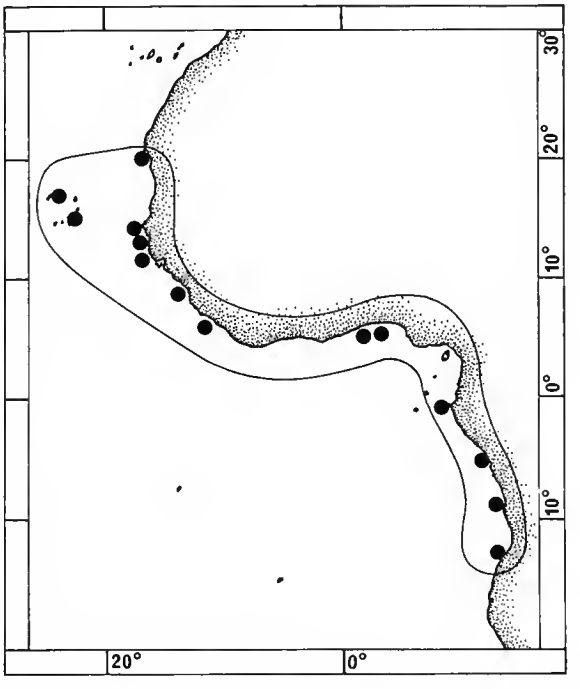


FIG. 27. — Box plots for Length to Height ratios of three samples of *Anadara geissei* from Angola, Guinea and the Cape Verde Islands.



MAP 7. — Distribution of *Anadara geissei*.

Anadara geissei is not greatly variable throughout its range but the data displayed in figure 27 shows that there is variation in the Length/Height ratio, with some examples from the Cape Verde Islands being much higher and therefore more quadrate and in which the posterior margin remains subauriculate. The choice of samples used suggests clinal variation with latitude but it could also be ecophenotypic. The material and ecological data are limited

and at this time we consider all forms to be nothing more than individual varieties of *A. geissei*. It should be noted that the unusual specimens approach the Caribbean *A. notabilis* (Röding, 1798), and LOCARD (1898) and LAMY (1907) record, in our view erroneously, this species from Cape Verde Islands and Senegal.

We consider that *A. geissei, A. floridana* and the panamic species *A. formosa* (Sowerby, 1833) to be closely related and that the west African and Panamic species are most similar. The subgenus *Rasia* Gray, 1857 is probably a useful taxon within the Atlantic/Panamic provinces but we are not certain of its relationship with Indo-Pacific forms. *A. geissei* is a semi-infaunal species forming extensive beds reminiscent of *Modiolus* and it is consequently rather different from the truly infaunal burrowing forms of more typical Anadarinae. The type species of *Anadara, A. antiquata* is similar in being much longer than high and one of us has (OLIVER, pers. obs.) noted that this species is also semi-infaunal although to a lesser degree. It is therefore inappropriate at this time to make a decision on the value of the subgenus *Rasia* world wide.

Anadara polii (Mayer, 1868)
(Pl. V, 1-9; fig. 30; map 8)

Arca antiquata Poli (*non* Linné, 1758), 1795 : 146, pl. 25, figs. 14-15.
Arca weinkauffi Crosse, 1862 : 324-325. *Nomen dubium.*
Arca diluvii auct. (non Lamarck, 1819 : 45).
Arca polii Mayer, 1868 : 75.
Arca diluvii var. *inflato-subglobosa* Aradas and Benoit, 1870 : 80.
Arca diluvii var. *elongato-depressa* Aradas and Benoit, 1870 : 80.
Arca (*Anadara*) *sphaerica* Kobelt, 1891 : 53-54, pl. 15, figs. 3-4.
Arca talismani Locard, 1898 : 308, pl. 8, figs. 21-24.
Arca polii var. *minor* Locard, 1898 : 305.
Arca polii var. *ventricosa* Locard, 1898 : 305.
Arca polii var. *curta* Locard, 1898 : 306.
Arca polii var. *transversa* Locard, 1898 : 306.
Arca polii var. *obliqua* Locard, 1898 : 306.
Arca polii var. *angulosa* Locard, 1898 : 306.

TYPE MATERIAL : The type material of *Arca weinkauffi* is uncertain : it was cited by CROSSE as being in the collection of WEINKAUFF, but later WEINKAUFF stated that it was never in his collection but was a single specimen in the Algerian Museum which had been stolen and replaced by a monstrosity of *Arca diluvii* (WEINKAUFF, 1880 : 200). Given this uncertainty we regard *A. weinkauffi* as a *nomen dubium.*

Anadara polii was erected by MAYER in order to distinguish the recent Mediterranean species from the Miocene *A. diluvii* Lamarck, 1819. His name was based on figures of the recent species in a number of early publications of which the earliest is that of POLI, 1795. Consequently we regard the figure of *A. antiquata* Linné in POLI to be the type.

The holotype of *A. sphaerica* is in SMF Frankfurt but it bears no locality data.

The type material of the varieties *inflato-subglobosa* and *elongato-depressa* are cited as in the collection of ARADAS and BENOIT but its present location is not known.

The holotype of *A. talismani* is in MNHN and has a slightly broken hinge plate which has been misrepresented in the original figure in LOCARD (1898).

TYLE LOCALITY : Sicily.

General description

We have encountered great difficulty in assessing the significance of the large range of morphological variation seen within this taxon. Individual populations or samples show little variation but between samples the extremes can be such that it is difficult to imagine that they are part of a single taxon. More over there is no apparent pattern to this variation such that we are unable to definitely invoke clinal, bathymetric or ecological causes to explain it. This species is restricted to rather deep water and we have mostly small samples of live collected material with the larger samples of dead valves only. This restricts our ability to assess the distribution of the variants and also introduces the concern that some of the samples are of subfossil origin, notably that of the large shells from Senegal.

In conclusion we have refrained from separating the morphs into nominal taxa and instead we present a general diagnosis which highlights the common features and also individual descriptions of the morphs. With further collection it may be possible to explain this variation or even to conclude that this group is a complex of closely related species.

Shell to 55 mm in length. Rather heavy. Slightly inequivalve when small, more or less equivalve in adult, LV a little larger. Inflated to greatly inflated, tumidity a little less than or a little greater than height. Inequilateral, beaks in the anterior 1/4 to 1/5. Outline oblong-subrectangular to suboval to ovate, usually longer than high but some only slightly so. Length/Height ratio varying from 1 : 1 to 1.3 : 1 (fig. 28). Posterior area weakly defined by rounded posterior angle; posterior margin oblique, curved to subtruncate. Median area deeply sulcate in post larval shell, otherwise rounded; ventral margin gently to deeply curved. Anterior area short to severely constricted. Length/Anterior to Beak Length varying from 2.9-4.7 (fig. 28); anterior margin broadly rounded.

Dorsal area moderately wide to wide. Ligament initially opisthodetic, developing anteriorly to fill dorsal area, chevrons widely spaced, few in number. Teeth numerous in two series.

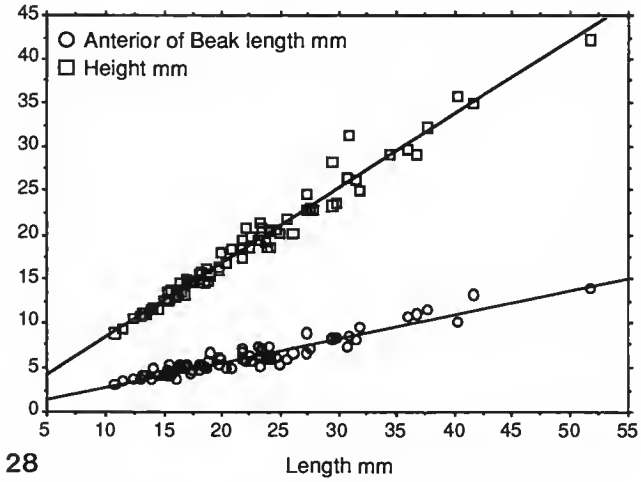
Sculpture of 24-28 (these include the small anterior and posterior dorsal riblets when apparent) radial ribs (fig. 29), these rather narrow, high and equal to or narrower than interspaces except down posterior angle where they may be wider. Rib sculpture discrepant; LV with closely spaced, rather small raised cross bars, RV similar but much weaker.

Periostracum reddish brown, with bristles in the interspaces, these are all rather soft and fragile, anterior and median areas with short sharply pointed triangular bristles, posterior angle with very long, narrow, linear bristles.

Morph descriptions

Anterior constricted morph (pl. V, 3B, 7, 8, 9) : Live collected shells to 25 mm. Inflated, tumidity only slightly less to slightly greater than height. Outline obliquely suboval, anteriorly constricted. Posterior margin oblique, gently curved, posterior ventral junction indistinct, rounded. Ventral margin curved, inclined towards the anterior and merging without a distinct junction into the broadly rounded anterior margin. Anterior area very small, sloping very steeply towards the umbo. Ligament extending anteriorly but not filling area completely.

Sculpture of 26-29, usually 27-28 ribs, all narrower than interspaces, noticeably steep sided and flat topped if not at all worn, LV sculpture delicate.



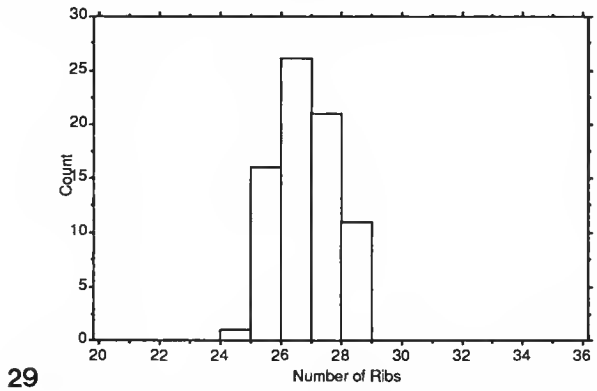


FIG. 28-29. — 28 : Plots of Total Shell Length against Height and Anterior to Beak Length for 75 shells of *Anadara polii* from throughout its range. 29 : Number of Ribs for 75 shells of *Anadara polii* from throught its range.

West African "subfossil" globose morph (pl. V, 3C, 4B) : Shells to 40 mm. Similar in outline to the above but some large shells are subspherical (probably gerontic). Sculpture of 24-28 ribs, usually 25-26 but this may be accounted for by wear of the posterior dorsal area. Ribs very noticeably narrower than interspaces. Ligament filling most of the dorsal area in large specimens.

Oblong morph (pl. V, 1A-B, 3A, 4A, 5, 6) : Shells to 55 mm in length. Inflated but tumidity distinctly smaller than height. Outline oblong-subrectangular; posterior and anterior ventral junctions distinct, especially posterior; ventral margin more or less parallel to dorsal margin. Sculpture of 26-27 ribs, the posterior a little wider; rib sculpture on LV prominent especially on small shells.

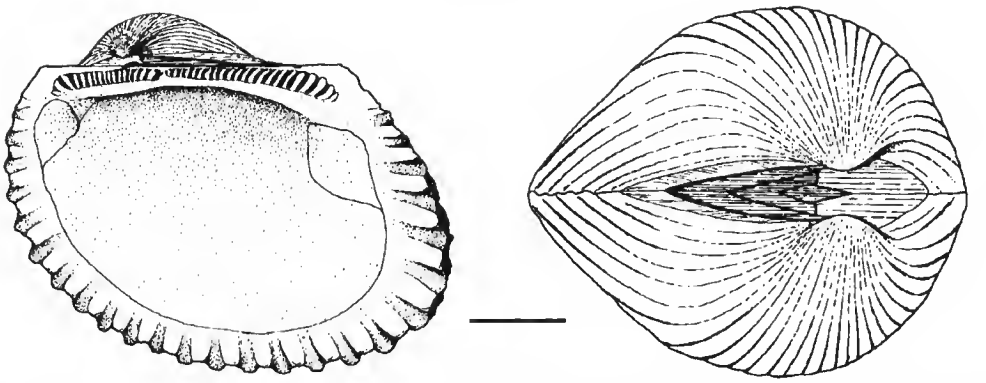
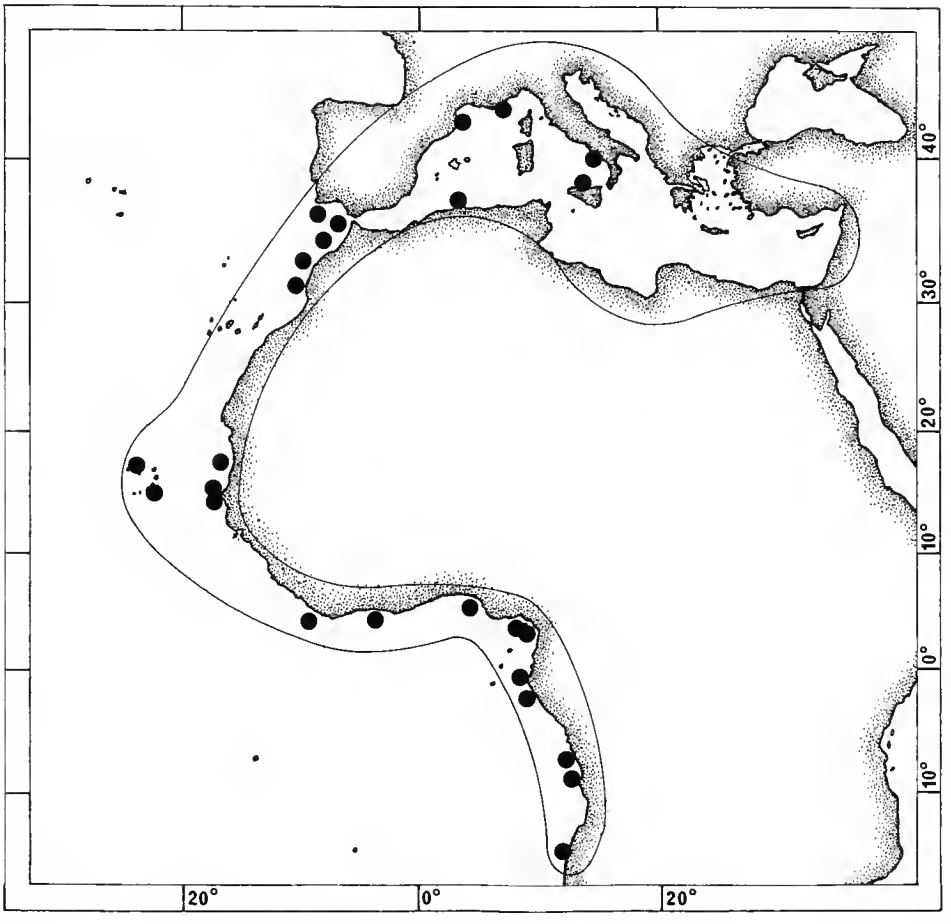


FIG. 30. — Internal view of right valve and dorsal view of *Anadara polii* (Mayer). Anteriorly constricted morph from Cameroon. (Scale bar = 5 mm.)

DISTRIBUTION : This species is recorded from Portugal (Setubal), throughout the Mediterranean south to Angola (Moçâmedes).

MATERIAL EXAMINED : **Mediterranean, Algeria** : No precise details, 2 spm. + 1 v., MNHN. **Italy** : Sicily, Palermo, 1 spm., leg. MONTEROSATO, 1914; S. Andrea, 2 spm., leg. del Prête, 1928-1929, coll. Staadt; Circeo-Tirreno, leg. TITTONI, 2.IV.1957, coll. Staadt; Naples, 5 spm., coll. PETIT, 1873; Naples, 1 spm., old coll.; all MNHN. **France** : St. Raphaël, 1 spm., coll. LOCARD, 1892; off Banyuls-sur-Mer, 130-190 m, 9 spm.; both MNHN. **Atlantic Morocco** : between 37°01′ N and 30°06′ N, 20-180 m, numerous spm., sh. and v. from 25 dredging stations of R/V "Vanneau", 1923-1929; between 36°49′ N and 33°43′ N, 144-332 m, numerous sh. and v. from 6 stations of R/V "Cryos", BALGIM, VI.1984; all MNHN. **Mauritania** : SW of Nouakchott, 17°44′ N/16°27′ W, 100 m, 2 v., dredged "Leon Coursin", leg. MARCHE-MARCHAD, 3.II.1957, MNHN. **Cape Verde Islands** : S. Vicente, 1 v.; off São Tiago, 15°16,5′ N/23°47,5′ W, 50-65 m, 1 v.; 15°26,5′N/23°14′ W, 100 m, 1 spm., all dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1959; all MNHN. **Senegal** : Off Cap Vert, 14 v.; off Cap Vert 200-300 m, 1 v.; off Kayar, 110-120 m, 12 v., all leg. MARCHE-MARCHAD, 1967; 15°38′ N/17°00′ W, 130 m, 1 v., dredged "Léon Coursin", leg. MARCHE-MARCHAD, 1.II.1957; 14°50,1′ N/17°29,3′ W, 150 m, many v., dredged "Tenace", leg. MARCHE-MARCHAD, 15.III.1967; 14°23,5′ N/17°24,5′ W, 65-70 m, 1 spm. + 8 v.; off Dakar, 50 m, 1 spm.; 200 m, 1 spm.; 129-150 m, 9 v.; S of Gorée, 110-112 m, 13 v., all dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 1954-1958; Casamance, 12°32′ N/28°8′ W, 45 m, fine sand, 2 v., dredged R/V "Louis Sauger", leg. VON COSEL, 28.III.1988; 14°15,8′ N/17°28′ W, 100 m, leg. LEUNG TACK; Thiaroye, NNE of Dakar, 7-8 m, leg. MARCHE-MARCHAD, 6.VI.1956; all MNHN. **Liberia** : 4°34,5′ N/8°31′ W, 64 m, 2 v.; 5°21,5′ N/9°54,5′ W, 73-80 m, 13 v., both dredged R/V "Calypso", leg. MARCHE-MARCHAD, 20.V.1956, all MNHN. **Côte d'Ivoire** : Off Abidjan, 1 spm. + 9 v.; off Abidjan, 60 m, 1 spm.; off Abidjan, 70 m, 4 spm., all leg. LE LOEUFF (ORSTOM); off Abidjan, 2 v., leg. MARCHE-MARCHAD; 4°50′ N/5°57′ W, 70 m, 7 v.; 5°01′ N/5°17′ W, 40 m, 1 spm., both dredged R/V "La Rafale", Guinean Trawling Survey, IV.1964; all MNHN. **Nigeria** : 4°00′ N/6°11′ E, 2 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. **Cameroon** : 3°54,5′ N/8°53′ E, 62-64 m, mud, 1 spm.; 3°54′ N/8°50′ E, 65-70 m, mud, 1 spm.; 2°51′ N/9°41′ E, 80 m, mud, 1 spm.; 2°39′ N/9°40′ E, 60-65 m, mud, 2 spm., all leg. CROSNIER, 22.VIII.1963; all MNHN. **Gabon** : Cap Lopez, on beach, 1 v., leg. CHEVALIER, 1984-1988; 0°32,8′ S/8°43,1′ E, 125-145 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. **Angola** : Off Ambrizete, Zaire province, 80 m, 4 v.; off Mussulo, Luanda province, 90-100 m, muddy ground, 12 v.; Ilha de Luanda, Luanda province, 120 m, many v.; Ilha de Luanda, 40-60 m, 2 v.; Ilha de Luanda, 90 m, 1 v.; Praia Amelia, Moçâmedes province, 40-60 m, 1 v., all leg. GOFAS, 1981-1984; all MNHN.

BIOTOPE : This species is restricted to offshore in depths from 50-200 m.



MAP 8. — Distribution of *Anadara polii*.

REMARKS

Of the morphs described the most common in tropical West Africa is the " anteriorly constricted " type. In West Africa living specimens are as yet all smaller than 25 mm which is half the size of those living in the Mediterranean. Considering the apparently subfossil samples the size ranges are more similar with a valve from Gabon reaching 40 mm. The most common type in the Mediterranean is the " oblong " morph but we have only 8 specimens and 1 valve from West Africa. Nowhere are the two extremes mutually exclusive and we cannot suggest that there is clinal variation. The globose morph represents many of the shells collected by the R/V " Vanneau " from off Morocco and is only rarely found in the Mediterranean. The large examples closely resemble the gerontic specimens of the subfossil samples from Senegal and

such specimens are the basis of both LOCARD's *A. talismani* and probably KOBELT's *A. sphaerica*.

The various morphs are shown to overlap in their distribution and there is a merging of one into the other when all samples are observed collectively. This degree of overlap can be seen in figures 31-32 which display the ranges of Length/Height and Length/Anterior/Beak Length ratios for shells from three parts of the range. These plots also show that the range of variation is greatest in the tropical West African shells. There is therefore no value in giving the morphs even varietal status and all are considered to be variants of *A. polii*.

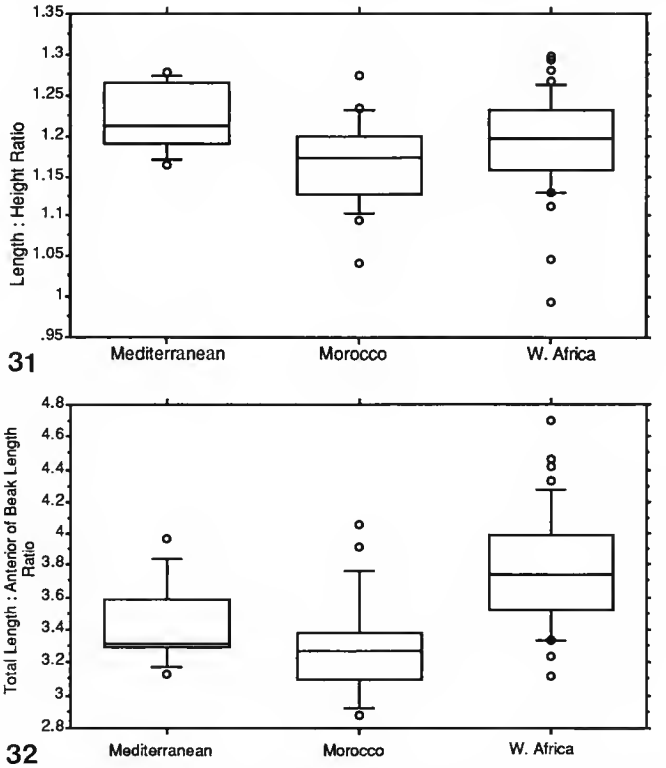


FIG. 31-32. — 31 : Box plots of Shell Length to Height ratios of shells of *Anadara polii* from three parts of its range, Mediterranean, Morocco and tropical West Africa. 32 : Box plots of Length to Anterior to Beak Length of shells of *Anadara polii* from three parts of its range, Mediterranean, Morocco and tropical West Africa.

We have chosen to use the name *A. polii* Mayer for this species and not the more often used *A. diluvii* Lamarck. We do not consider that from our examination of the types of *A. diluvii* this species to be the Miocene/Pliocene counterpart of the Recent form because (i) the rib number is 33 not 24-28, (ii) the beaks are situated much more closely to the midpoint, (iii) the ribs are equal in width to the interspaces.

Anadara eborensis n. sp.
(Pl. VI, 1A-D; fig. 33; map 9)

TYPE MATERIAL : Holotype (31.9 mm), MNHN, off Grand Bassam, Côte d'Ivoire, 5°07′ N/3°22′ W, 20 m, dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, 21.III.1964. Paratypes : MNHN, off Grand Lahou, Côte d'Ivoire, 5°00′ N/5°28.5′ W, 27 m, 1 spm., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956; NMWZ, Guinea, 9°36′ N/14°12′ W, 21 m, 1 spm., dredged R/V "André Nizery", leg. VON COSEL, 19.V.1988.

TYPE LOCALITY : Côte d'Ivoire, off Grand Bassam.

DESCRIPTION

Shell to 32 mm in length. Heavy. Slightly inequivalve, LV a little larger. Inflated, almost as tumid as high, strongly umbonate. Inequilateral, beaks almost in the anterior quarter.

Outline subquadrate, only slightly longer than high. Posterior area broad sloping steeply, set off by strong but rounded posterior angle; posterior margin obliquely subtruncate, more or less straight; posterior ventral junction distinct, sharply rounded. Median area narrow, more or less flat except in very earliest stages in which it is deeply sulcate, ventral margin gently curved or more or less straight. Anterior margin broadly rounded. Dorsal margin straight, anterior junction almost 90°, posterior junction oblique.

Dorsal area broad, slightly cleft or more or less flat, umbonal separation wide. Ligament initially developing with a single posterior chevron, then adding anteriorly towards the beaks and eventually in front of the beaks but chevron number remaining low with up to 5 growth points on the hinge line, chevrons narrow.

Hinge plate moderately thick, teeth in two series, separation slight with posterior set pushing over the anterior, anterior set up to 24 teeth, posterior set up to 27 teeth. Teeth laminar, narrow, vertical.

Sculpture of 24-27 (usually 25) radial ribs, these narrow and only half the width of the interspaces, steeply angled with narrower, rather flat top; RV weakly nodulose, LV almost smooth.

Periostracum rust brown with slightly darker, short, thorn like, recurving bristles arising from the interspaces of the anterior and median areas; those on the posterior angle all worn.

Shell white.

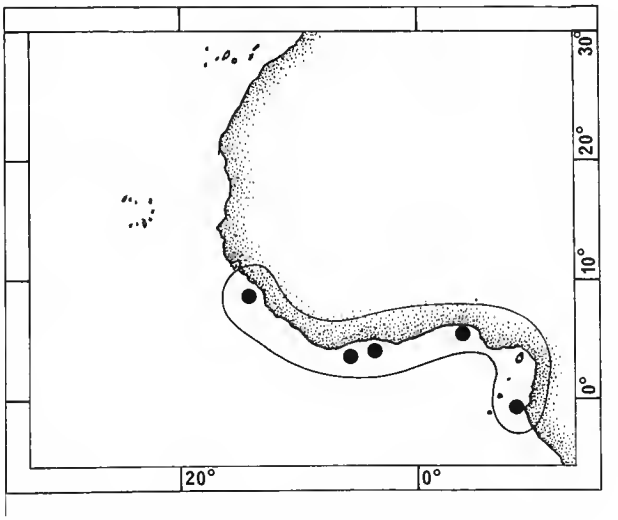
Adductor muscle scars unequal, the posterior considerably larger. Internal margin deeply crenulate.

SELECTED SHELL MEASUREMENTS : See in Remarks section under *Anadara subglobosa*.

DISTRIBUTION : This species has a restricted distribution from Guinea to Côte d'Ivoire and Gabon.

MATERIAL EXAMINED : The type material; **Guinea** : 9°40′ N/14°05′ W, 18 m, many v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956; 9°12′ N/13°43,5′ W, 24 m, 1 spm.; 9°01′ N/13°30′ W, 12 m, 1 spm., both dredged R/V "André Nizery", leg. VON COSEL, 27.IX.1988; all MNHN. **Liberia** :

4°34,5′ N/8°31′ W, 64 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. **Côte d'Ivoire** : 5°03′ N/5°25′ W, 20-25 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 21.V.1956; off Abidjan, 2 spm., dredged R/V "Reine Pokou", leg. LE LOEUFF (ORSTOM); both MNHN. **Nigeria** : 4°34,5′ N/8°31′ E, 64 m, 1 v.; 4°03′ N/6°12′ E, 32 m, 1 v., both dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. **Gabon** : Cap Lopez, 3 v., leg. CHEVALIER, 1984-1988, MNHN.



MAP 9. — Distribution of *Anadara eborensis*.

BIOTOPE : This species has been dredged from mud and mixed muddy substrates offshores from 18 to 64 m.

DERIVATIO NOMINIS : *eborensis*, Latin, derived from *eboris*, "ivory" with the suffix *ensis* denoting place referring to the type locality of the Côte d'Ivoire.

REMARKS : The heavy subquadrate appearance of this shell is reminiscent of other species placed in the subgenus *Larkinia* but those species have a true amphidetic ligament. The only Caribbean species with any similarity is *Anadara brasiliana* but it also has a truly amphidetic ligament, the ribs are as broad as the interspaces and the rib sculpture is more prominent. Most akin to *A. eborensis* is perhaps *A.* (*Esmerarca*) *reinharti* Lowe, 1935, both in the general shape, the form of the ligament and the weak discrepant rib sculpture. The posterior margin of *A. reinharti* by comparison is rounded, there is a slight posterior ventral sinuation and the ribs are as wide or wider than the interspaces.

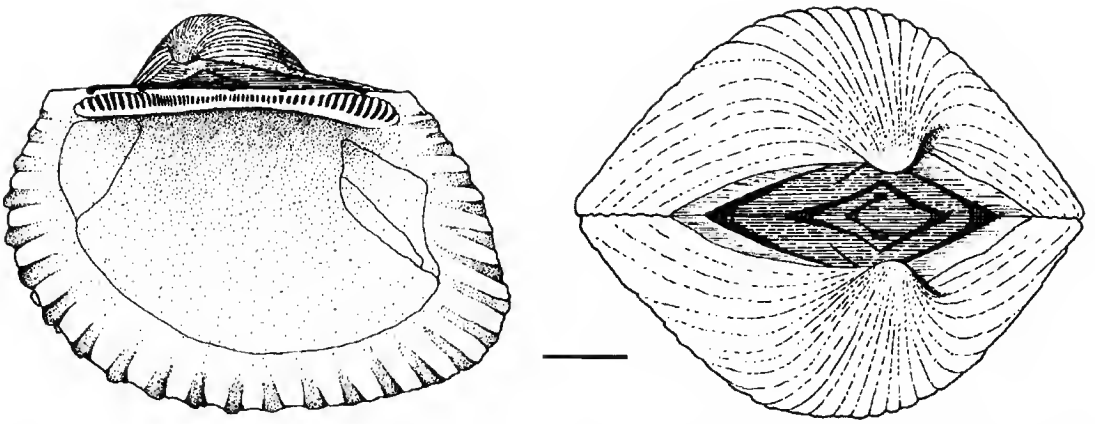


FIG. 33. — Internal view of right valve and dorsal view of *Anadara eborensis* n. sp. Côte d'Ivoire. (Scale bar = 5 mm.)

Anadara subglobosa (Dunker, 1891)
(Pl. VI, 2A-B; fig. 34; map 10)

Arca (*Anomalocardia*) *subglobosa* Dunker in KOBELT, 1891 : 99, pl. 26, figs 7-8.

TYPE MATERIAL : Most probably in ZMB Berlin. In the MNHN we have located a single specimen in the BAVAY collection which is marked as coming from VON MALTZAN, collected at Gorée, Senegal. This agrees with the data available with the type as cited by DUNKER and also agrees with his figure (1891 : pl. 26, fi.g. 8).

TYPE LOCALITY : Gorée, Senegal.

DESCRIPTION

Shell to 19 mm in length. Slightly inequivalve in juveniles, more or less equivalve in adults. Inflated to strongly inflated, usually with tumidity less than height but some adults with tumidity greater than height, umbonate but not greatly. Inequilateral, beaks in the anterior 1/3 to 1/4.

Outline subrectangular, adults always distinctly longer than high with the anterior half of the shell a little more expanded than the posterior, juveniles less so. Posterior area relatively short, sloping rather steeply and demarcated by a distinct, acutely rounded posterior angle but this is not so marked in the juveniles; posterior margin oblique, moderately long, more or less straight; posterior ventral junction distinct, roundly acute. Median area strongly sulcate in post larval shell and to a lesser degree in juveniles to about 8 mm, otherwise gently curved; ventral margin gently curved, subparallel to dorsal margin. Anterior area small, anterior margin broadly rounded, anterior ventral junction obsolete. Dorsal margin straight.

Dorsal area rather wide, more so anterior to the beaks, umbonal separation moderate to wide. Ligament initially opisthodetic but very rapidly developing anteriorly and appearing

secondarily amphidetic except for a small anterior ligament free area; chevrons very few, 2-3 in number, very narrow.

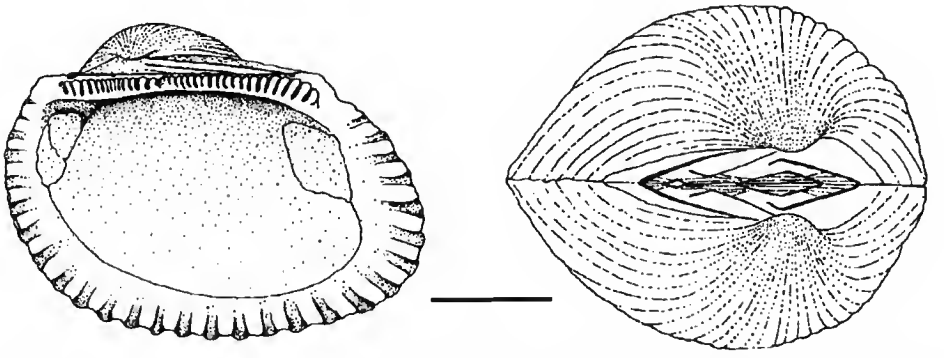


FIG. 34. — Internal view of right valve and dorsal view of *Anadara subglobosa* (Dunker). Mauritania. (Scale bar = 5 mm.)

Hinge plate moderately thick; teeth in 2 series, the anterior set pushing below the posterior at their junction; anterior set up to 18 teeth, posterior set up to 24 teeth. Teeth laminar, all teeth vertical except for a few slightly oblique posterior marginals.

Sculpture of 28-31 radial ribs, these narrower than interspaces in adults with steeply angled sides and a rather flat topped appearance. Rib sculpture discrepant, stronger on LV of rather long, sparse nodules, RV more or less smooth except for weak nodules on anterior ribs. Interspace sculpture distinct of widely spaced concentric, crescentric notches.

Periostracum rarely preserved in a good state; generally rust brown in colour with sparse bristles in the interspaces; anterior and median bristles thorn-like recurved dorsally; on posterior angle longer, narrower.

Shell white.

Adductor scars unequal, the posterior twice the size of anterior, posterior quadrate; anterior rounded, often a little raised. Inner margin deeply crenulate.

SELECTED SHELL MEASUREMENTS : See below in Remarks section.

DISTRIBUTION : From Mauritania (17° N) south to Côte d'Ivoire.

MATERIAL EXAMINED : **Mauritania** : 17°30′ N/16°15′ W, 41 m, 1 spm., dredged R/V "N'Diago", leg. RICHER DE FORGES, 1981, MNHN. **Senegal** : Gorée, 1 spm., coll. BAVAY ex coll. VON MALTZAN; Gorée, 1 spm., coll. JOUSSEAUME; SE of Gorée, 14°41′ N/17°23,2′ W, 17 m, fine sand and mud, 2 v., dredged R/V "Louis Sauger", leg. VON COSEL, 24.III.1988; S of Gorée, 65 m, many v.; 110-112 m, 1 v.; 95-98 m, many v.; SW of Cap Manuel, 50 m, 1 v., all dredged "Gérard Tréca", leg. MARCHE-MARCHAD, II.1954; 14°50′ N/17°29′ W, 150 m, dredged "Tenace", leg. MARCHE-MARCHAD, 15.III.1967; 14°31,9′ N/17°13,5′ W, 28 m, 1 spm., coll. LEUNG TACK, 1983-1984; Casamance, Abéné, 13°01,8′ N/17°25,5′ W, 53 m, hard ground and fine sand, 1 v.; 12°46,6′ N/17°19,2′ W, 32 m, carbonate and fine sand, 1 v., all dredged R/V "Louis Sauger", leg. VON COSEL, 28-29.III.1988; 14°2,5′ N/17°09,1′ W, 24 m, 2 v., dredged "Cdt. Henri Gomis", leg. BODARD, 7.XII.1966; 13°01′ N/17°24′ W, 51-55 m, 1 spm. + 2 v., dredged, R/V "Calypso", leg. MARCHE-MARCHAD, 1956; all MNHN. **Ghana** : 4°57′ N/2°42′ W, 40 m, muddy ground, 1 spm. + 1 v., dredged R/V "La Rafale" Guinean Trawling

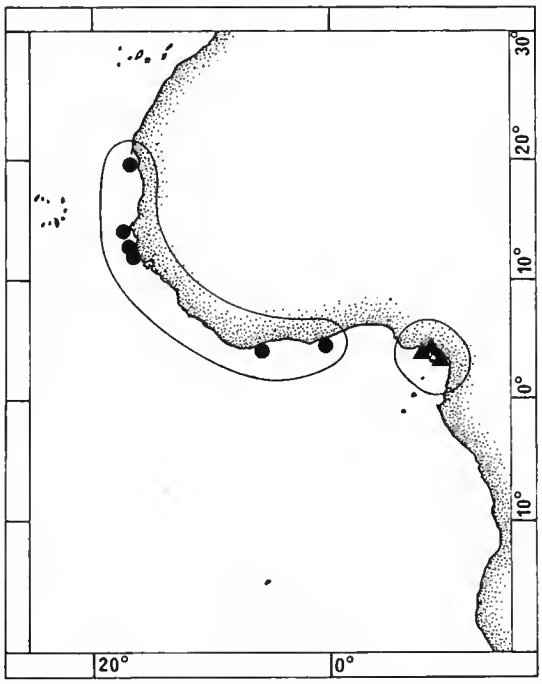
Survey, leg. CHERBONNIER, 19.III.1964; MNHN. **Côte d'Ivoire** : 4°52,5′ N/5°57,5′ W, 40 m, hard ground and calcareous algae, 2 v.; 5°05′ N/3°22′ W, 30 m, mud, sand and shell gravel, 2 spm. + 4 v.; 5°07′ N/3°22′ W, 20 m, 1 spm.; all dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, III and IV.1964; all MNHN.

BIOTOPE : This species has been collected primarily in deep water from 17-200 m.

REMARKS

This species is clearly related to *Anadara eborensis* (this paper) by the similarity in growth of the ligament and the shape and sculpture of the radial ribs. It differs from that species in being rectangular rather than quadrate, that is with a larger Length/Height ratio (fig. 35); and also less tumid (fig. 35).

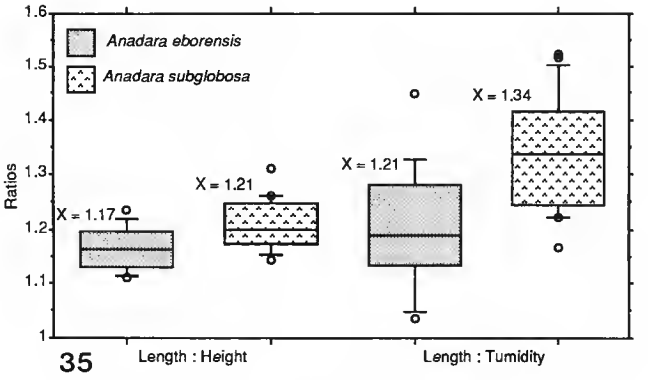
Although there is a degree of overlap with these characters the rib number is consistently different between the two species *A. subglobosa* having more ribs, 28-31 as against 24-27 for *A. eborensis* (fig. 36).



MAP 10. — Distribution of *Anadara subglobosa* (circles) and *A. camerunensis* (triangles).

The distribution of these species overlap, and we have not found intermediate samples in the material at hand. It is of interest to note that it does seem possible to distinguish non overlapping morphologies in some groups yet not in others. The degree of plasticity in shell form within the *Anadara* group has never been explained but is well illustrated by referring to

any of the major works on the Tertiary faunas of Europe or the Caribbean where a multitude of forms are described. Until we have understanding of this plasticity the species systematics will remain fraught with difficulty so long as we are limited to traditional conchological methods. With the Recent fauna recourse to electrophoretic and genetic methodology could be advantageous.



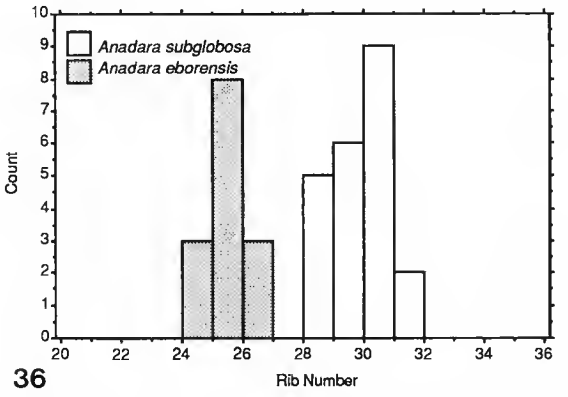


FIG. 35-36. — 35 : Box plots of Length to Height and Length to Tumidity ratios for *Anadara eborensis* (n = 14) and *A. subglobosa* (n = 20). 36 : Bar chart of rib number in *Anadara eborensis* (mode 25) and *A. subglobosa* (mode 31).

Anadara senegalensis (Gmelin, 1791)

(Pl. VI, 3A-D, 4A-B, 5A-B; pl. VII, 1-4; fig. 39; map 11)

"Le Robet" Adanson, 1757 : pl. 248, fig. 6.
Arca senegalensis Gmelin, 1791 : 3312.
Arca pertusa Reeve, 1844 : Sp. 28, pl. V.

TYPE MATERIAL : Lectotype (here selected), MNHN, from coll. ADANSON, a left valve, 20 mm in length. This is not the valve cited by FISCHER-PIETTE (1942) as the figured specimen in ADANSON (1757) but we argue that the original figure is so poor that it does not adequately represent any of the specimens labelled by ADANSON as "Le Robet". Furthermore the two valves cited by FISCHER-PIETTE are not a pair,

the right valve does not fit into the left valve and the widths of the dorsal areas are different. Paralectotype as lectotype, 2 valves.

TYPE LOCALITY : Senegal.

DESCRIPTION

Shell to 25 mm in length. Inequivalve, LV larger than RV. Greatly inflated, tumidity almost equal to or a little greater than height; strongly umbonate. Inequilateral, beaks in the anterior third.

Outline rhomboidal-oval, initially a little longer than high, later almost as high as long. Posterior area very short and very steep; posterior angle distinct but rounded; posterior margin long, a little oblique, almost vertical, gently curving in juveniles but with a subtle angulation in adults. Median area curved except in post larval shells which are sulcate; ventral margin curved, posterior ventral junction slightly angulate, anterior ventral junction not marked but curving into anterior margin which is short, weakly curved and almost vertical. Dorsal margin straight, rather short.

Dorsal area slightly cleft, rather narrow, umbonal separation slight. Ligament initially opisthodetic, later apparently amphidetic but with a somewhat larger anterior ligament free area, chevrons widely spaced, numbering up to 4.

Hinge plate thick, teeth in two series, separation slight, anterior set up to 22 teeth, posterior to 20 teeth. Teeth laminar, some weakly chevron shaped, all more or less vertical.

Sculpture discrepant, of 23-24 radial ribs, LV with anterior 15-16 ribs strongly nodulose formed by thickened crossbars, RV with anterior 6-10 ribs more weakly nodulose.

Periostracum a thin rust brown coating except for spicate bristles arising from interspaces, on posterior area of closely spaced, thin, long, black, erect bristles; on median area of shorter wider bristles directed posteriorly.

Shell white.

Adductor scars unequal, posterior twice as large as anterior, pedal retractor scars small indistinct. Inner margin strongly crenulate corresponding to radial sculpture.

SELECTED SHELL MEASUREMENTS : See figure 37.

Casamance variety (pl. VII, 3-4) : This larger (to 29 mm) variant differs from the typical form in being distinctly longer than high and is therefore oblong-rhomboidal in outline. The sculpture is slightly weaker but the nodules are still large if not so raised. The shell is thinner and consequently the hinge plate is weaker and the teeth smaller. This is the form represented by ADANSON's type specimens.

DISTRIBUTION : This species has been recorded from Guinea south to Angola (Bengo province).

MATERIAL EXAMINED : **Senegal** : No precise locality, 4 spm., coll. H. FISCHER; Dakar, 2 v., coll. CHEVALIER, 1900; N. Casamance, Kafountine, beach to the south, 4 v., Abéné-Kafountine, beach, many v.; S. Casamance, Cap Skirring-Diembéring, on beach, many v.; Cap Skirring, beach to the south, many v.; Bôlon opposite Elinkine, 3 m, 8 v.; off Kafountine, 3-6 m, 1 v.; Katakalous Bôlon, 2-4 m, 1 v.; S of Cap Skirring, 3-5 m, many v., all leg. VON COSEL, 5-17.III.1988; off Cap Skirring, 12°22,5′ N/17°03′ W,

20 m, 2 v.; off Cap Skirring, 12°23′ N/16°52,8′ W, 13 m, 5 v.; 12°46,9′ N/17°29,9′ W, 45 m, many spm., all dredged R/V "Louis Sauger", leg. VON COSEL, 27-29.III.1988, all MNHN. **Guinea-Bissau** : Casamance border, Essoukoudiak Bôlon, 5-6 m, 2 v., leg. VON COSEL, 7.III.1988; 11°58,5′ N/16°59′ W, 14 m, 3 spm.; 11°53′ N/16°56,5′ W, 11 m, 2 spm.; 12°05′ N/17°02,5′ W, 14 m, many spm., all dredged R/V "André Nizery", leg. VON COSEL, 7.X.1988; all MNHN. **Guinea** : No precise locality, 2 spm., coll. PARFAIT, 1889; Cap Varella, 3 v., coll. MAUNY, 1964; Conakry, many v., coll. DUFOSSÉ, 1905; all MNHN. **Côte d'Ivoire** : Off Abidjan, 1 spm., leg. MARCHE-MARCHAD; Sassandra, Batebré beach, many v., coll. AUBERT DE LA RUE, 1950; off Abidjan, 4°50′ N/5°57′ W, 70 m, 8 v., dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, 4.IV.1964; off Bassam, 20 m, 1 spm.; Abidjan region, 20-26 m, 27 spm. + 1 sh. from 4 stations, all dredged R/V "Reine Pokou", leg. LE LOEUFF (ORSTOM), 1966-1967; all MNHN. **Togo** : Lomé, 14 v., MNHN. **Gabon** : No precise locality, 1 sh., coll. H. FISCHER; Cap Lopez, beach south of lighthouse point, 6 v., leg. CHEVALIER, 1984-1988, both MNHN. **R.P. Congo** : Off Conkouati, 4°00′ S/10°59′ E, 19 m, many v.; 4°10′ S/11°15′ E, 19 m, 1 spm., both trawled "Kounda", leg. VON COSEL, XII.1985; Pointe-Noire, Plage Mondaine, many v.; Plage Raffinerie, 6 v., Plage ORSTOM, 2 v.; Baie de Pointe Noire, off Plage ORSTOM, 5-7 m, many spm., dredged from muddy fine sand; 3-4 m, 5 spm. + many v., dredged from fine sand and gravel; off Plage Mondaine, 5 m, 3 v., dredged from muddy fine sand; off Songolo, 5-6 m, 1 v., dredged from muddy fine sand, off Plage Raffinerie, 1 m, 3 v., all leg. VON COSEL, X-XII.1985; all MNHN. **Angola** : Cacuaco, Bengo province, 0-10 m, 1 spm. + 5 sh. + 6 v.; Moçâmedes, Moçâmedes province, 0-2 m, 1 v.; Ponta do Mussulo, Luanda province, on beach, 1 v., all leg. GOFAS, 1981-1985, all MNHN.

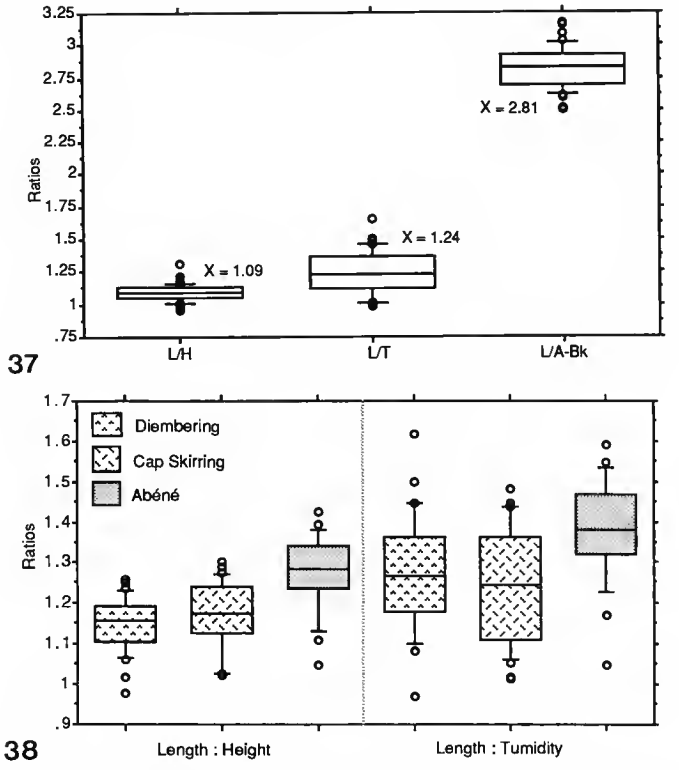
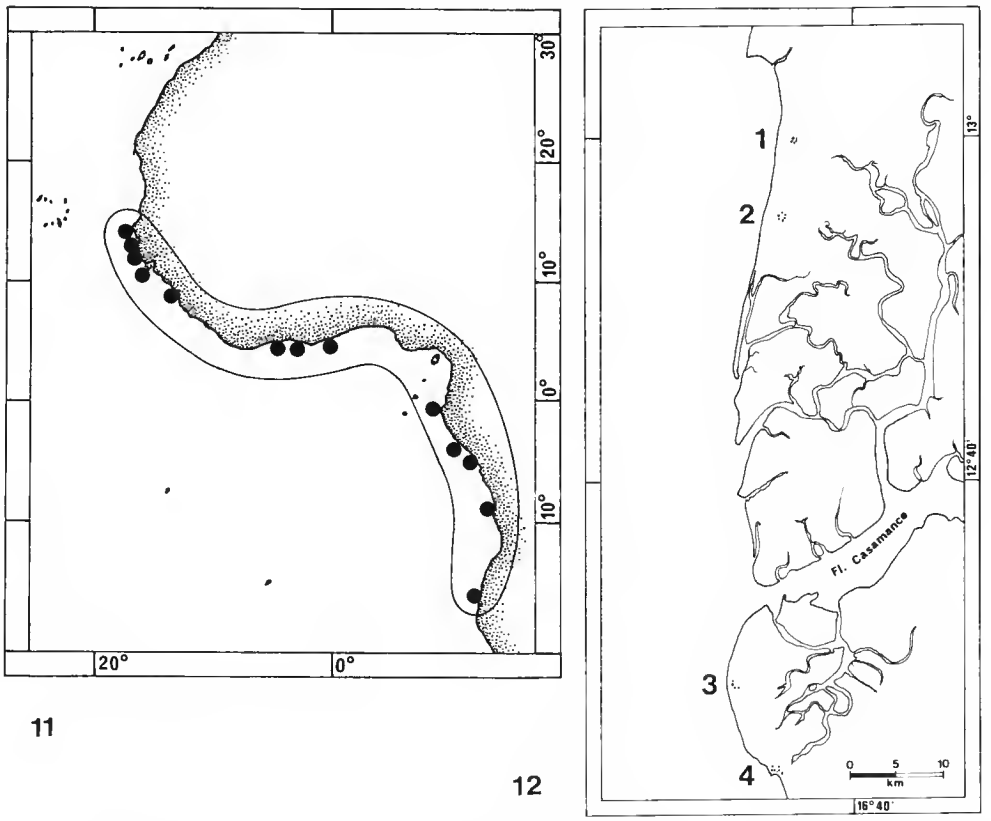


FIG. 37-38. — 37 : Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Anadara senegalensis* typical form from Guinea-Bissau, Côte d'Ivoire and R.P. Congo (n = 59). 38 : Box plots of the ratios of Total Shell Length to Height and Tumidity of three samples of *Anadara senegalensis* from the Casamance region of West Africa (n = 20 per sample).

Biotope : Live collected material of this species has been collected in shallow depths from the sublittoral to 30 m.



Map 11-12. — 11 : Distribution of *Anadara senegalensis*. 12 : Coast of Casamance with the localities of *Anadara senegalensis*. **1.** Abéné; **2.** Kafountine; **3.** Diembéring; **4.** Cap Skirring. Scale = 10 km.

Remarks

This is the most frequently encountered *Anadara* in the West African material examined, and for most of its range it is well defined and not variable. There are, however, a number of samples principally from the Casamance district of Senegal but also some from the R.P. Congo and the northern provinces of Angola that include a rather different form. This form is described above as the Casamance variant.

We are fortunate to have a few large samples of beached valves from Casamance (map 12) and the Length/Height and Length/Tumidity ratios are plotted in figure 38. This shows that the sample (Abéné) from the northern part, close to the Gambia River, contains more "Casamance" variants than those from further south, south of the Casamance River, but that the two forms are not mutually exclusive. The fact that the « Casamance » variant is

also to be found around the Congo river indicates that this may not be clinal variation but is perhaps linked to environmental conditions close to the estuaries of large rivers. Much more detailed collecting would be needed to assess whether or not the "Casamance" variant is truly linked to these ecological conditions.

One factor ANOVA table for Length to Height ratios of three samples of *Anadara senegalensis* from the Casamance region.

One factor ANOVA, 2 degrees of freedom, F = 15.934, p = .001.

Group	Count	Mean	Std. Dev
Dimbéring	30	1.149	.067
Cap Skirring	30	1.17	.086
Abéné	22	1.273	.095

Comparison	Mean Diff.	Scheffe F-test
Diembéring vs Cap Skirring	—.021	.51
Diembéring vs Abéné	—.125	14.56*
Cap Skirring vs Abéné	—.103	9.979*

* Significant at 95 %.

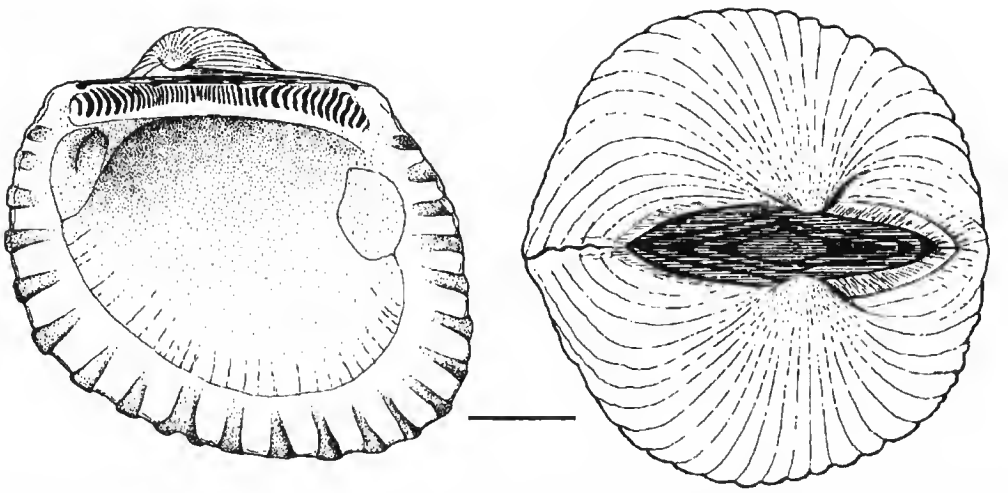


FIG. 39. — Internal view of right valve and dorsal view of *Anadara senegalensis* (Gmelin). Typical adult shell from Côte d'Ivoire. (Scale bar = 5 mm.)

The ANOVA table for the Length to Height ratios shows a statistically significant difference between the Abéné sample (from the North) and those from Cap Skirring and Diembéring (from the South). However over the total range the Casamance variant and the typical form grade into each other. The use of such analyses for the separation of taxa can be misleading and in general for *Anadara* species other non continuous variables such as rib number should always be considered.

Anadara senegalensis would from its general form be considered to belong the subgenus *Cunearca* but it differs in the form of the ligament which has many chevrons and is secondarily

amphidetic. The ligament of the type species of *Cunearca* (*Arca incongrua* Say, 1822) consists of an amphidetic sheet of fibrous ligament with a single outer lamellar chevron. This form of ligament is also found in *Anadara chemnitzi* Philippi, which is the closest Caribbean counterpart to *A. senegalensis*, and in *Anadara pilula*, a similar Indo-Pacific species. The significance of such differences in ligament structure have never been considered within the Anadariinae, and it is not known whether it should be given any phylogenetic credence.

Anadara camerunensis n. sp.

(Pl. V, 6A-C; fig. 43; map 10)

TYPE MATERIAL : Holotype (15.1 mm), MNHN, Cameroon, Victoria (now Limbe)-Bota, 8-10 m, leg. VON COSEL, 4.XII.1985. Paratypes : as holotype, 3 spm.; NMWZ, Cameroon, Victoria-Bota, 5-6 m, leg. VON COSEL, 4.XII.1985, 2 spm.

TYPE LOCALITY : Cameroon, Victoria (now Limbe).

DESCRIPTION

Shell to 16.4 mm in height. Inequivalve, LV larger than RV. Greatly inflated, tumidity almost as great as length; strongly umbonate. Inequilateral, beaks in the anterior third.

Outline obliquely-oval, subrhomboidal, higher than long. Posterior area short, very steeply sloping; posterior angle prominent but rounded; posterior margin very long, slightly oblique, very gently curved. Median area rounded except in post larval shells which are sulcate; ventral margin curving into anterior margin which is broadly rounded, posterior ventral junction roundly angulate. Dorsal margin straight.

Dorsal area slightly cleft, wider in front of beaks, umbonal separation moderate. Ligament initially opisthodetic, later apparently amphidetic but ligament free area a little large anteriorly, chevrons few, widely spaced, numbering up to 3.

Hinge plate thick, teeth in two series, separation indistinct, anterior set up to 17 teeth, posterior set up to 17 teeth. Teeth laminar or slightly chevron shaped, more or less vertical.

Sculpture of 21-22 radial ribs, discrepantly nodulose; RV with the anterior 9-11 ribs nodulose, LV with anterior 13-14 ribs strongly nodulose, all nodules as raised cross bars across whole of rib.

Periostracum a thin coating, dark rust brown in colour except for interspaces which bear erect bristles, on the posterior area these are very long rigid black hairs, elsewhere much shorter and wider.

Shell white.

Adductor scars unequal, posterior twice the size of the anterior, pedal retractor scars indistinct. Inner margin deeply crenulate corresponding to radial ribs.

SELECTED SHELL MEASUREMENTS

Length (mm)	Height (mm)	Tumidity (mm)	Anterior to beak (mm)	Hinge line to ventral (mm)	Rib No.	Locality
15.1	16.4	14.9	5.4	12.3	[9/13] 21	Cameroon, 8-10 m
12.6	13.2	12.6	4.2	9.8	[11/14] 22	
12.4	13.2	11.7	4.0	10.3	[10/14] 22	
11.6	12.0	10.1	3.8	9.1	[10/14] 22	
11.1	12.7	11.3	3.9	9.7	21	Cameroon, 24 m
12.4	13.2	12.2	3.7	10.6	21	Cameroon, 5-6 m

(The numbers in square brackets mark the nodulose ribs in RV and LV.)

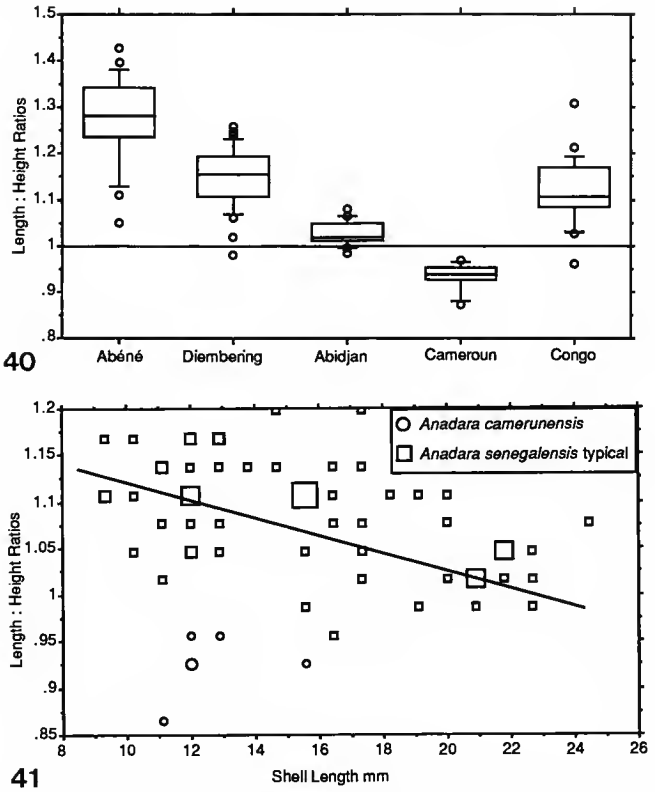


FIG. 40-41. — 40 : Box plots of Length to Height ratios for samples of *Anadara senegalensis* [Abéné (n = 20), Diembéring (n = 20), Abidjan (n = 20) and Congo (n = 23)] and *A. camerunensis* [Cameroon (n = 6)]. 41 : Graph of Length to Height ratios plotted against Shell Length for *Anadara senegalensis* (n = 130) and *A. camerunensis* (n = 6). Overlapping points are shown as increasing symbol sizes.

DISTRIBUTION : This species is restricted to the coast of Cameroon.

MATERIAL EXAMINED : **Cameroon** : Victoria/Limbe-Bota, 8-10 m, 5 v., leg. VON COSEL ; off Victoria, 3°44′ N/9°11′ E, 24 m, 1 spm ; between Wouri estuary and Cap Nachtigal, 3°44′ N/9°22′ E, 13 m, 1 v., both trawled "Campo Star", leg. VON COSEL, XII.1985 ; all MNHN.

BIOTOPE : This species is infaunal and inhabits muddy fine sand from 5 to 24 m.

DERIVATIO NOMINIS : *camerunensis* after the Republic of Cameroon, the type locality.

REMARKS

We have considered at length that this species might be an ecomorph of *Anadara senegalensis*, however we can find no environmental parameters that would give rise to the changes observed. In *A. camerunensis* the adult size is only 16 mm as compared to 35 mm for *A. senegalensis*. For most of its ontogeny *A. camerunensis* is higher than long which is the case for only the occasional specimens of *A. senegalensis* (fig. 40-41).

The rib number, although not greatly different, is totally consistent : that of *A. camerunensis* from 21-22 and for *A. senegalensis* 23-24 (fig. 42).

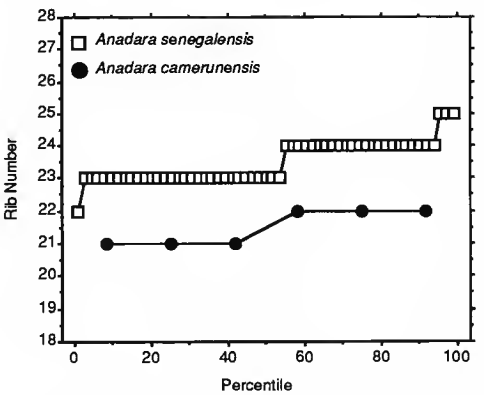


FIG. 42. — Rib Number frequency data for *Anadara senegalensis* (n = 130) and *A. camerunensis* (n = 6) shown as percentile line plots.

Comparing the adults of each, *A. camerunensis* is more oblique, the posterior ventral margin being more attenuated. Overlaps with *A. senegalensis* have not yet been found, and we have consequently given this form specific status.

Anadara camerunensis has its closests counterpart in the Panamic province, *A. nux* (Sowerby, 1833), but differs in the form of the ligament. In *A. nux* there is a single outer chevron (fig. 43C) bounding a large median sheet, and the growth is amphidetic. This type of ligament is found in none of the West African Anadarinae included in this paper but is not uncommon in the Panamic, Caribbean and Indo-Pacific. The shape of the shell of *A. nux* and *A. camerunensis* would place them in *Cunearca*. However, should the adaptive form of the shell

be given greater phyletic weight than the form of the ligament? This problem requires a complete cladistic analysis of the Anadarinae and highlights the inconsistency in the current generic systematics.

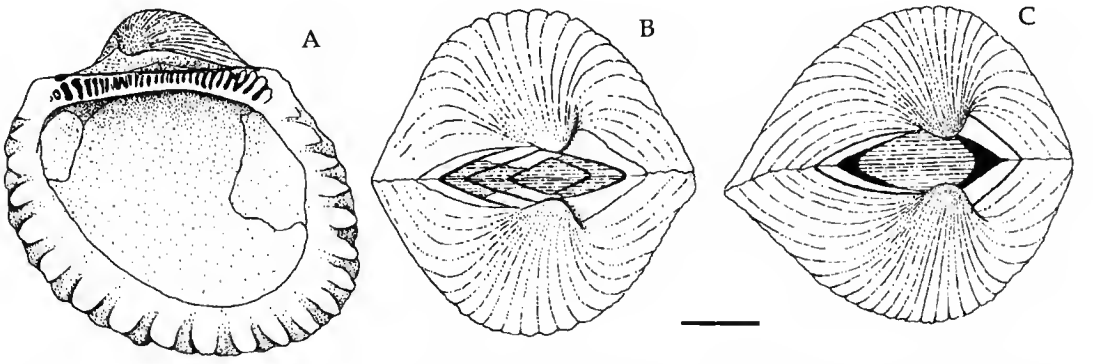


FIG. 43. — A-B, Internal view of right valve and dorsal view of *Anadara camerunensis* n. sp. Cameroon; C, Dorsal view of *Anadara nux* (Sowerby). Ecuador. (Scale bar = 3 mm.)

Anadara corbuloides (Monterosato, 1878)
(Pl. VII, 5A-D; fig. 46; map 12)

Arca corbuloides Monterosato, 1878 : 67.

TYPE MATERIAL : Not located.

TYPE LOCALITY : Algeria.

DESCRIPTION

Shell to 70 mm in length. Inequivalve, LV larger than RV, most noticeable in small specimens, obsolete in the larger examples. Inflated, tumidity normally a little greater than half the length but in gerontic specimens much greater. Inequilateral, beaks in the anterior half.

Outline subelliptical, longer than high. Posterior area poorly defined; posterior angle rapidly becoming obsolete; posterior margin evenly rounded except for a small indentation at the posterior dorsal junction. Median area rounded but sulcate in post larval shell; ventral margin curved lacking angles with anterior and posterior margins. Anterior margin broadly rounded to obliquely curved, some becoming rather straight resulting in a subacute anterior dorsal junction. Dorsal margin relatively long, straight.

Dorsal area becoming wide, slightly cleft, umbonal separation moderate. Ligament initially opisthodetic becoming secondarily amphidetic; chevrons few, widely separated, numbering up to 5.

Hinge plate rather narrow, teeth in two series, separation indistinct, anterior set up to

37 teeth, posterior to 39 teeth. Teeth small, pointed, larger teeth slightly chevron shaped, most vertical, a few lateral teeth a little oblique.

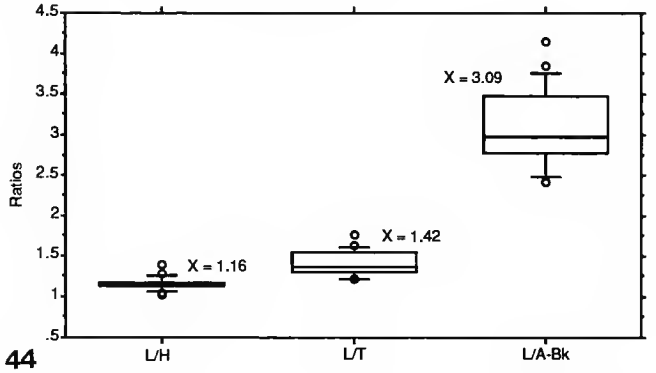
Sculpture of 30-35 radial ribs; rib sculpture discrepant, RV with a few anterior ribs with very weak nodules or ridges, LV with all but posterior area ribs distinctly but not strongly nodulose.

Periostracum a thin coating, rust to olivaceous brown in colour except for interspaces which bear umbonally directed rigid spicate bristles.

Shell white.

Adductors scars subequal. The posterior a little larger. Inner margin deeply crenulate.

SELECTED SHELL MEASUREMENTS : See figure 44.



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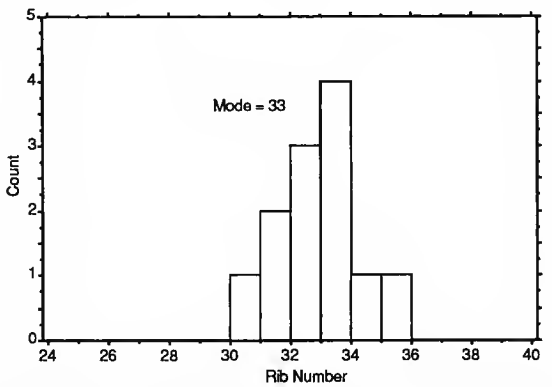

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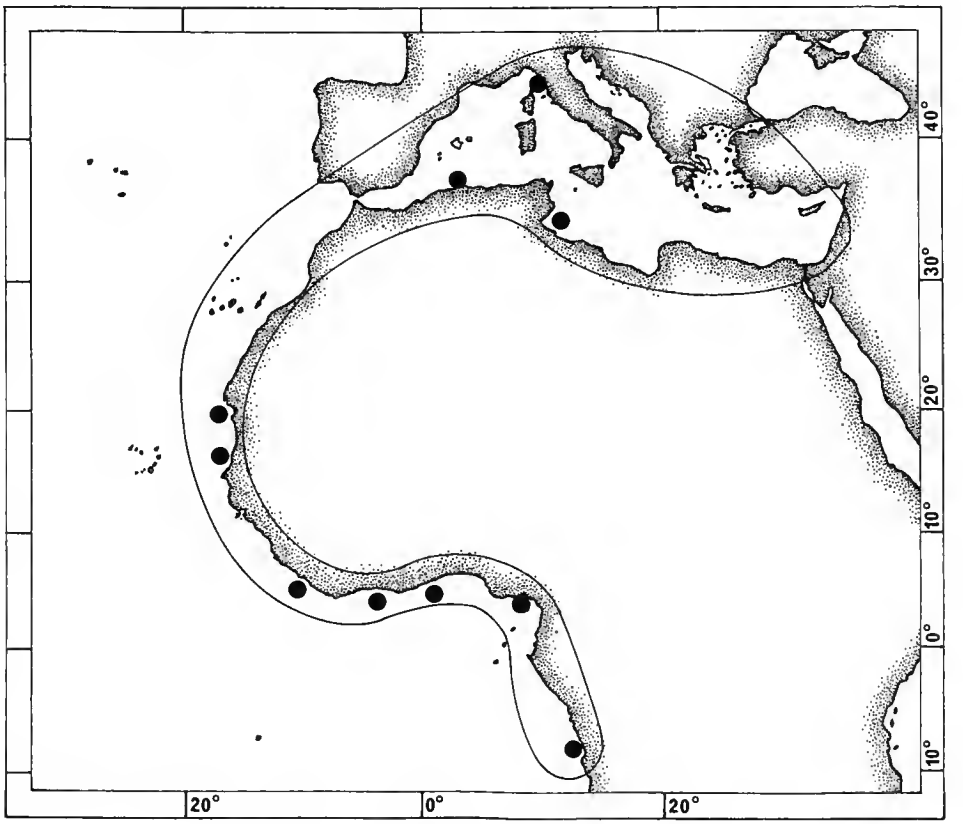
FIG. 44-45. — 44 : Box plots of the ratios of Total Shell Length to Heigth (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Anadara corbuloides* (n = 12). 45 : Bar chart of Rib Number for 12 shells of *Anadara corbuloides*.

DISTRIBUTION : This species ranges throughout the Mediterranean and from Spain (Cadiz, HIDALGO, 1916) along the West African coast and south to northern Angola (Luanda), but is nowhere common.

MATERIAL EXAMINED : **Algeria** : No precise locality, 1 spm., leg. JOLY, 1921, MNHN. **Tunisia** : Gulf of Gabes, N. of Djerba, beach, 1 v., leg. BOUCHET and WARÉN, 1982, MNHN. **Italy** : Viaregio, 2 spm., coll. DEL PRÊTE, MNHN. **Mauritania** : 17°42′ N/16°16′ W, 54 m, 1 spm., dredged R/V " N'Diago ", leg. RICHER

DE FORGES, 1981, MNHN. **Senegal** : Kayar, north of Dakar, 110-120 m, 1 v., leg. MARCHE-MARCHAD, 6.IV.1967; 14°30,6′ N/17°18,9′ W, 43 m, 1 v., leg. LEUNG TACK, 1983-1984, both MNHN. **Liberia** : 4°34,5′ N/8°31′ W, 64 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. **Côte d'Ivoire** : Off Abidjan, 1 v., leg. MARCHE-MARCHAD, MNHN. **Ghana** : 4°40′ N/2°08′ W, 50 m, 1 spm., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. **Cameroon** : Between Wouri estuary and Cap Nachtigal, 3°43′ N/9°13′ E, 32-35 m, 1 v., trawled "Campo Star", leg. VON COSEL, 22-29.XI.1985, 2°23′ N/9°41′ E, 45 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, both MNHN. **Angola** : Off Ponta das Lagostas, Bengo, province, 30-50 m, 2 spm., leg. GOFAS, MNHN.



MAP 13. — Distribution of *Anadara corbuloides*.

BIOTOPE : *Anadara corbuloides* lives in fine muddy sand or mud, well offshore from 30 m to 60 m and occasionally deeper.

REMARKS : *Anadara corbuloides* apparently has two counterparts in the Panamic Pacific province, namely *A. mazatlanica* (Hertlein and Strong, 1943) and *Scapharca* (*Caloosarca*) *biangulata* (Sowerby, 1833). The fact that these species are placed in different genera by KEEN (1971) shows how the use of the equivalve condition gives rise to anomalous supraspecific classification. In *A. corbuloides* the juveniles are distinctly inequivalve but this condition becomes obsolete with ontogeny.

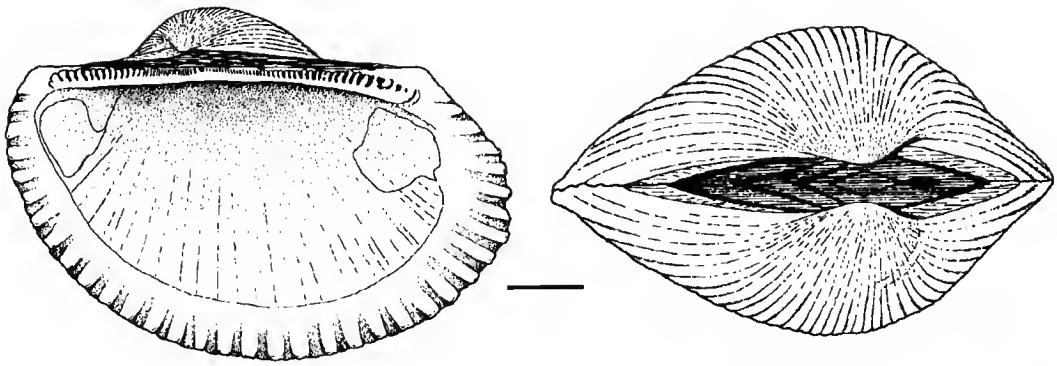


FIG. 46. — Internal view of right valve and dorsal view of *Anadara corbuloides* (Monterosato). Angola. (Scale bar = 10 mm.)

Genus **SENILIA** Gray, 1842

TYPE SPECIES : *Arca senilis* Linné, 1758 (SD Gray, 1847).

Senilia senilis (Linné, 1758)
(Pl. VIII, 1A-B, 2, 3; fig. 49; map 13)

Arca senilis Linné, 1758 : 694.

TYPE MATERIAL : One specimen in the Linnean collection, London (DODGE, 1952 : 151).

TYPE LOCALITY : "Jamaica" (10th edition) but later emended to "O. Africano" (12th edition).

DESCRIPTION

Shell to 135 mm in length. Equivalve at all sizes. Inflated about the umbos but wedge shaped in cross section; moderately to strongly umbonate. Inequilateral, beaks in the anterior third, strongly prosogyre.

Outline subrhomboidal-trigonal, anteriorly expanded, posteriorly to some degree attenuate. Posterior area not defined; posterior angle weak; posterior margin oblique, slope variable from 30° to 65°. Median area rather flat, never sulcate even in post larval sizes; ventral margin more or less straight, posterior ventral junction subacute to attenuate. Anterior margin broadly rounded. Dorsal margin relatively short, straight.

Dorsal area short, more or less flat to cleft, rhomboidal with anterior area much more broad. Ligament initially opisthodetic, developing beyond the beaks 20 mm and secondarily amphidetic in large or old shells; chevrons strong, numbering up to 8.

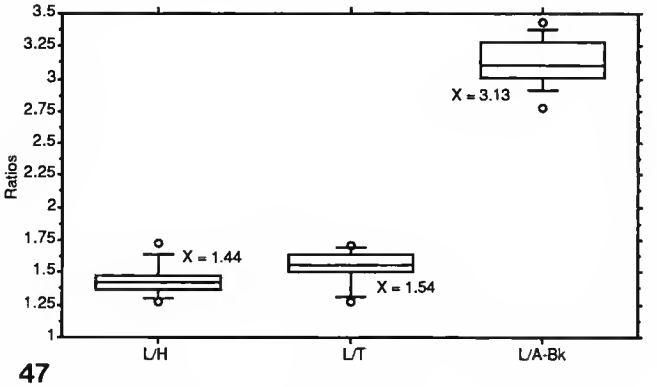
Hinge plate becoming massive, teeth in two series, separated by a narrow oblique gap; anterior set up to 15 teeth, posterior set up to 16 teeth. Teeth long weakly chevron shaped but often becoming divided or distorted, mostly more or less vertical.

Sculpture of 13-15 broad flattened smooth ribs, occasionally narrowed and more rounded especially in the least attenuate shells.

Periostracum persistent, a thin coating with very fine concentric thickenings in the interspaces. Colour initially olivaceous then reddish brown to black.

Shell white.

Adductor scars subequal. Inner margin with large crenulations.



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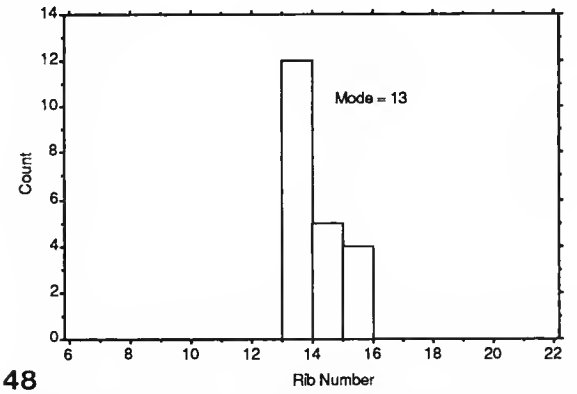

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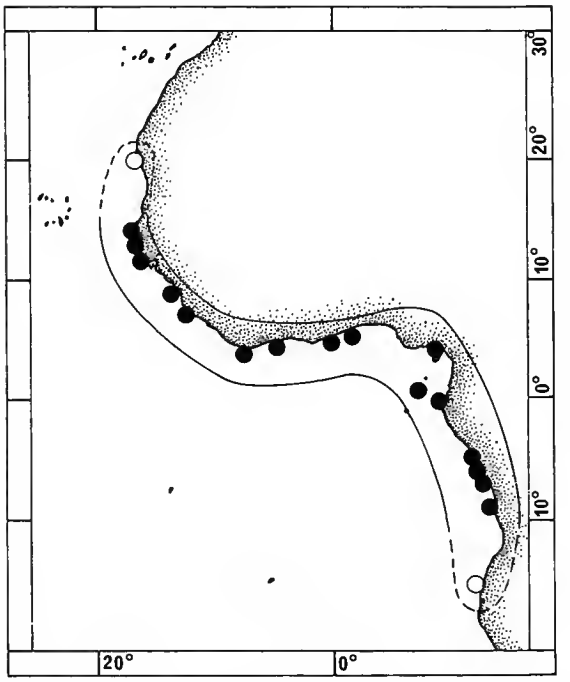
FIG. 47-48. — 47 : Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Senilia senilis* (n 21). 48 : Bar chart of Rib Number for 21 shells of *Senilia senilis*.

SELECTED SHELL MEASUREMENTS : See figure 47.

DISTRIBUTION : This species ranges from West Sahara (Rio de Oro) south to Angola.

MATERIAL EXAMINED : **Mauritania** : Port Étienne (now Nouadhibou) to Nouakchott, many v., from 12 sta., all subfossil, Miss. GRUVEL, 1908, MNHN. **Senegal** : Dakar, Marigot de Hann, 2 sp., 1 v., Miss. GRUVEL, V.1908; Sine-Saloun region, mangroves, 8 spm., leg. BOUCHET, 9.VIII.1973; S-Casamance : Katakalous Bôlon, muddy sand, 3-4 m, many juv. spm.; Ourong Bôlon, on sandbank, low tide, 1 spm.,



MAP 14. — Distribution of *Senilia senilis*. The empty circles indicates records of valves with subfossil appearance.

1 v.; Karabane, sandbank, 2 sh., all leg. VON COSEL, III.1988; all MNHN. **Gambia** : 1 sp., coll. D'AUGUSTIN, 1835, MNHN. **Sierra Leone** : Sierra Leone River, 1 spm., leg. LONGHURST, 13.X.1954, MNHN. **Liberia** : Cap des Palmes, 2 sh., old coll., MNHN. **Côte d'Ivoire** : Azuretti Lagoon, Grand Bassam, 1 v., leg. AUBERT DE LA RUE, 1950, MNHN. **Ghana** : Accra, on beach, 3 v., Miss. GRUVEL, 26.I.1910, MNHN. **Benin** : Icheppê-Olokun, 3 v.; Lac Abénué, 1 sh., both Miss. GRUVEL, 1910, MNHN. **São Tomé** : Off Punta Oquedelrey, 5 m, 3 sh., 3 v., all juv., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. **Cameroon** : Victoria/Limbe, on beach, 6 sh., leg. VON COSEL, XII.1985, MNHN. **Gabon** : Baie de Cap Lopez, 3 sh., Miss. GRUVEL, 1910, MNHN. **R.P. Congo** : Cocobeach, 1 sh., coll. SOYER, 1969; Loango, 6 sh., Office Pointe-Noire, 1969; Pointe-Noire, Plage Mondaine, on beach, 1 v., leg. VON COSEL, XII.1985, all MNHN. **Zaïre** : Crique de Moanda, 1 sh., leg. Miss. GRUVEL, 1910, MNHN. **Angola** : Cabinda, 1 sh., leg. C. R. BOETTGER, 1909; Ponta do Mussulo, Luanda province, on beach, many sh.; Baia dos Tigres, Moçâmedes province, 1 sh., both leg. GOFAS, 1981-1985, all MNHN.

BIOTOPE : *Senilia senilis* is a typical marine-estuarine species with lives in sandy mud, fine muddy sand or fine sand in estuaries, lagoons and creeks with regular tidal and seasonal salinity changes, often in the vicinity of mangroves, where it may be found in great quantities. It tolerates reduced salinity as well hyper salinity and lives predominantly in the lower intertidal zone.

REMARKS : This species is quite variable in outline with some shells distinctly attenuate posteriorly and others rather shortened. In the latter this compression results in the ribs being narrower, more rounded and more elevated (pl. VIII, 3). The functional morphology of this species was discussed by YONGE (1955) and the recent and fossil ecology by DEBENAY and SY (1989).

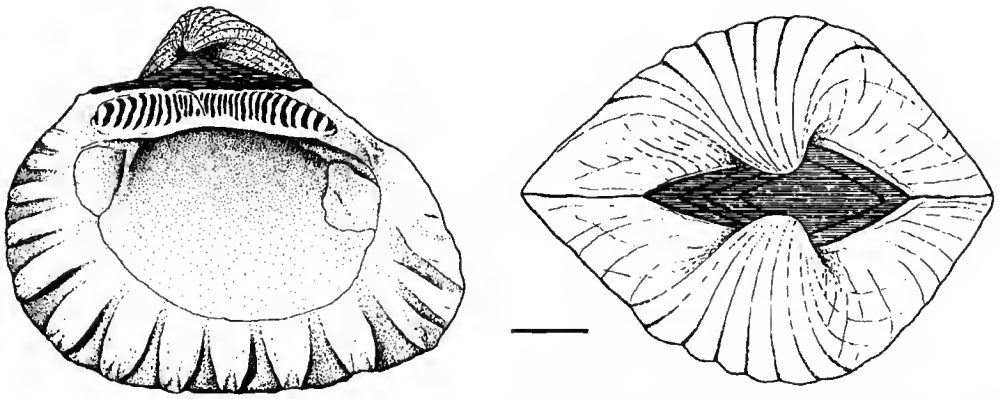


FIG. 49. — Internal view of right valve and dorsal view of *Senilia senilis* (L.). Angola. (Scale bar = 5 mm.)

Genus **BATHYARCA** Kobelt, 1891

TYPE SPECIES : *Arca pectunculoides* Scacchi, 1834 (OD).

DIAGNOSIS : The genus *Bathyarca* is placed in the Anadarine by NEWELL (*in* MOORE, 1969), but, as shown by OLIVER and ALLEN (1980), the genus contains both epibyssate and endobyssate species thus encompassing the range of morphology exhibited by both the Arcinae eg. *Barbatia* and the Anadarinae eg. *Scapharca*, The unique feature of the genus is the mantle extension which is present to some degree regardless of shell shape. This is one of the few examples in the Arcidae where a group of species can be isolated by a synapomorphy and consequently it is a more rigid group than either the Arcinae or Anadarinae. There may therefore be a case for raising the genus to subfamily level and creating genera to separate the epibyssate species from the endobyssate species (OLIVER, in prep.).

Bathyarca grenophia (Risso, 1826)
(Pl. VII, 4; fig. 50)

Arca grenophia Risso, 1826 : 313.
Arca pectunculoides Scacchi, 1834 : 82.

TYPE MATERIAL : Holotype (1 valve) of *A. grenophia* in MNHN Paris; type material of *A. pectunculoides* not located.

TYPE LOCALITY : Not cited; here selected Nice, Mediterranean France.

DESCRIPTION

Shell to 6 mm in length. Inequivalve, RV fitting into LV, not greatly inflated. Inequilateral, beaks in the anterior half.

Outline suboval, posteriorly expanded. Posterior area indistinct, posterior angle rapidly becoming obsolete, posterior margin broadly rounded. Median area flattening or weakly

sinuate, ventral margin rounded, usually with an indentation at the byssal exit. Anterior margin rounded but distinctly narrower than posterior. Dorsal margin straight.

Dorsal area narrow, umbonal separation weak. Ligament of few chevrons restricted to behind the beaks.

Hinge plate weak, teeth in two series separated by a distinctly edentulous space, anterior set up to 5 teeth, posterior set up to 8 teeth. Teeth small, straight, lateral teeth becoming strongly oblique.

Sculpture weak, subcancellate. Periostracum weakly haired. Shell white.

DISTRIBUTION : Throughout the Atlantic and in the subarctic from Norway to Angola in the east and from Greenland to Bermuda in the west.

MATERIAL EXAMINED : **Ibero-Maroccan Gulf** : 36°46′ N/07°07′ W, 368-371 m, 5 spm. + 2 v.; 36°36′ N/07°24′ W, 478-491 m, 1 spm.; 36°15′ N/08°01′ W, 1340-1263 m, 15 spm.; 35°54′ N/06°13′ W, 133-137 m, 1 v.; 35°54′ N/06°14′W, 150 m, 3 spm.; 36°41′ N/07°19′ W, 543-544 m, 4 spm.; 35°54′ N/06°14′ W, 293 m, 6 spm.; 35°35′ N/03°45′ W, 480 m, 5 spm.; 35°31′ N/07°26′ W, 1209-1302 m, 2 spm.; 35°26′ N/04°19′ W, 170 m, 1 spm.; 34°24′ N/07°31′ W, 1203 m, 1 spm.; 34°21′ N/07°24′ W, 885-895 m, 6 spm.; 33°49′ N/08°24′ W, 255-267 m, 5 spm.; 33°46′ N/08°30′ W, 309 m, many spm.; 33°45′ N/08°32′ W, 345 m, 1 spm., 6.VI.2984, all dredged R/V "Cryos", BALGIM campaign, all MNHN. **Senegal** : 230° off Cap Manuel, 120-215 m, many v. + 1 sh., in stomach of holothurian; off Dakar, 14°27′ N/17°33′ W, 150-250 m, many v.; 14°53′ N/17°30′ W, 205-230 m, 1 spm. + 3 v.; 170-200 m, 3 spm. + 19 v.; Baie de Gorée, 80-250 m, 14 v.; SW of Gorée, 150-250 m, 5 v., all dredged "Gérard Tréca", leg. MARCHE-MARCHAD, 1954-1958; all MNHN. Also based on the material used by OLIVER and ALLEN (1980).

BIOTOPE : This species lives attached to hard substrates and secondary hard substrates in soft sediment areas such as small stones, dead shells, worm tubes etc. In the north of its range it is found in the sublittoral zone as shallow as 2 m but further south it submerges to become a bathyal species and off the west African coast is found from 100-1300 m.

REMARKS : Comparing the west African material and more typically that from the greater end of the depth range with the northern shallow water material it is noted that the former possesses a thinner almost translucent shell in which the sculpture is very weakly developed. In these respect it resembles the form *pellucida* described by OLIVER and ALLEN (1980) from similar depths off the eastern American coast. Also amongst the BALGIM material from the Ibero-Maroccan gulf are many specimens of *Bathyarca obliqua* Philippi. This species is larger and more elongate than *B. grenophia* with a resultantly longer hinge line. It also ranges further north to boreal waters but as yet it has not been recorded from the west African coasts south of Morocco.

Bathyarca inaequisculpta (Smith, 1885)
(Pl. VIII, 5; fig. 51)

Arca (*Scapharca*) *inaequisculpta* Smith, 1885 : 267, pl. 17, figs. 8a-d.
Bathyarca dakarensis Locard, 1898 : 321, pl. 8, figs. 25-28.

TYPE MATERIAL : Syntypes in BMNH. The syntypes of *B. dakarensis* are in MNHN.

TYPE LOCALITY : Off Culebra Islands, West Indies. The type locality of *B. dakarensis* is off Dakar, Senegal.

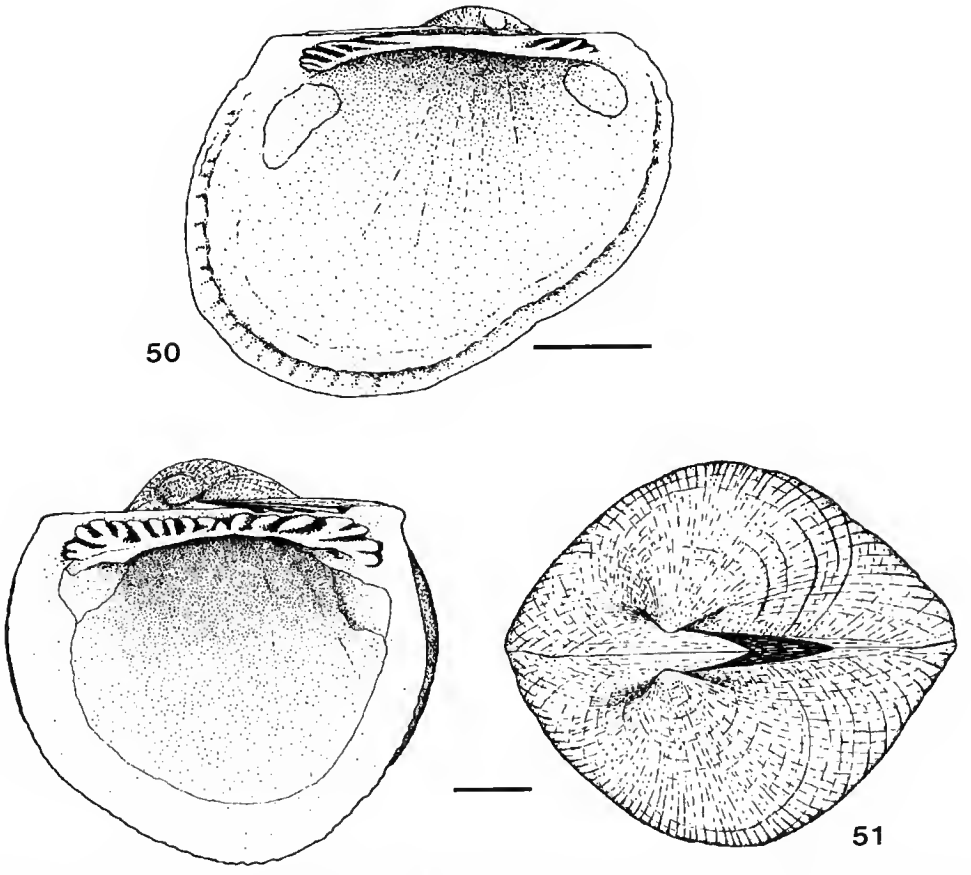


FIG. 50-51. — 50 : Internal view of left valve of *Bathyarca grenophia* (Risso). Senegal, 150-250 m. 51 : Internal view of right valve and dorsal view of *Bathyarca inaequisculpta* (Smith). Angola, 3797 m. (Scales bars = 1 mm.)

DESCRIPTION

Shell to 8 mm in length. Inequivalve. Inflated. Inequilateral, beaks in the anterior half.

Outline subcircular, as high or higher than long. Posterior area and posterior angle not demarcated. Margins other than dorsal not differentiated, round. Dorsal margin relatively long and straight. Median area curved, not sulcate.

Dorsal area narrow, umbonal separation slight. Ligament with few chevrons restricted to behind the beaks.

Hinge plate narrow, teeth in two séries but separation obscure, anterior set up to 8 teeth, posterior set up to 10 teeth. Teeth small, straight, lateral teeth becoming strongly oblique.

Sculpture weak, finely decussate, often a little stronger RV. Periostracum weak, sparsely pilose. Shell white.

DISTRIBUTION : This species is widely distributed in bathyal and abyssal zones throughout the Atlantic Ocean from 50 N to 14° S.

MATERIAL EXAMINED : The material examined is that used by OLIVER and ALLEN (1980).

BIOTOPE : This is a truly deep sea species and is confined to abyssal oozes in which it lives at or near the surface anchored to sediment particles by a multi threaded byssus. Although it has been found as shallow as 700 m it is more typically abyssal ranging from 1900-5000 m.

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PLATE I

1A-D. — *Arca noae* Linné : West Sahara, off Cap Barbas, 21°05'N/17°14'W, 43-45 m, MNHN. 73 mm. 1A, periostracum removed.

2. — *Arca noae* Linné : Cape Verde Islands, Ilha do Sal, Santa Maria, on beach, MNHN. 11.5 mm.

3A-D. — *Arca bouvieri* Fischer : Angola, Cacuaco, Bengo province, 5-10 m, MNHN. 60 mm. 3A, periostracum removed.

4. — *Arca bouvieri* Fischer : Angola, Corimba, Luanda province, 10-20 m, MNHN. 11 mm.

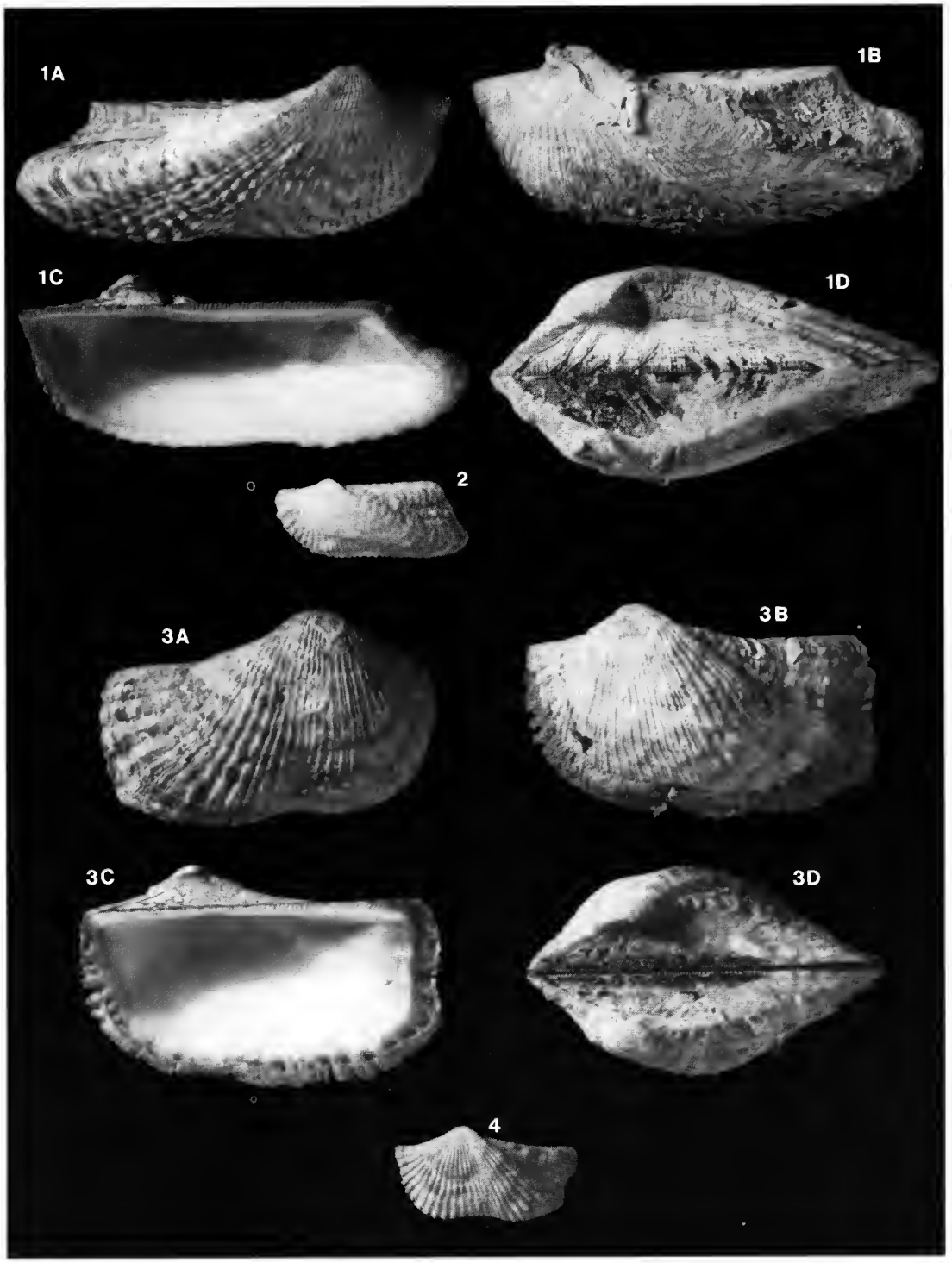

PLATE I

PLATE II

1A-D. — *Arca avellana turbatrix* n. ssp. : Holotype. Angola, Santo Antonio, Benguela province, intertidal, rocks. MNHN. 31 mm. 1A, periostracum removed.
2. — *Arca avellana turbatrix* n. ssp. : Paratype. Angola, Lucira, Moçâmedes province, MNHN. 18.7 mm.
3A-B. — *Arca imbricata* Bruguière : Florida, NMWZ. 50 mm. 3A, periostracum removed.
4. — *Arca avellana* Lamarck : Seychelles, MNHN. 30 mm, periostracum removed.
5A-B. — *Arca tetragona* Poli : Ireland, Berehaven, Bantry Bay, NMWZ. 21.3 mm.
6. — *Arca tetragona* Poli : England, Falmouth, NMWZ. 26.6 mm.
7A-B. — *Acar plicata* (Dillwyn) : Cape Verde Islands, Mindelo, São Vicente, MNHN. 7A, 19.1 mm ; 7B, 18.2 mm.
8A-B. — *Acar pulchella* (Reeve) : Mediterranean, Algeria, MNHN. 18.2 mm.

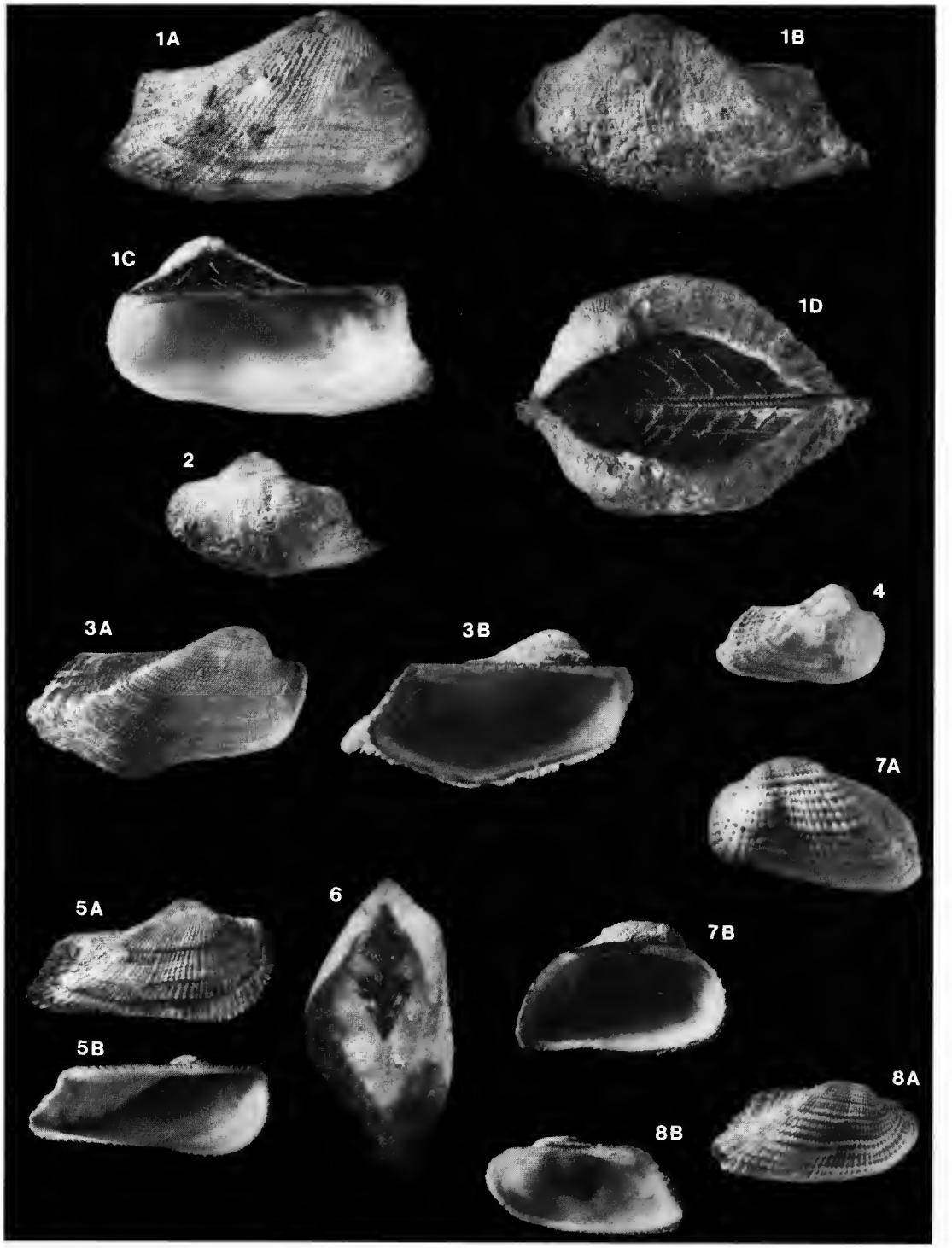

PLATE II

PLATE III

1A-B. — *Barbatia complanata* (Bruguière) : Côte d'Ivoire, Canal de Vridi, Abidjan, MNHN. 1A, 51 mm ; 1B, 18 mm.
2. — *Barbatia complanata* (Bruguière) : Angola, Chapeu Armado, Moçâmedes province, rocks at low tide, MNHN. 40 mm.
3. — *Barbatia complanata* (Bruguière) : Angola, Caotinha, Benguela province, MNHN. 33 mm.
4. — *Barbatia complanata* (Bruguière) : Angola, Lucira (Praia do Cesar), Moçâmedes province, MNHN. 45 mm.
5A-B. — *Barbatia complanata* (Bruguière) : Angola, Praia Amelia, Moçâmedes province, rocks at low tide, MNHN. 5A, 22 mm ; 5B, 16 mm.
6A-B. — *Barbatia gabonensis* n. sp. : Holotype. Gabon : off Mayumba, 3°25′ S/9°56′ E, 100 m, MNHN. 27.7 mm.
7A-B. — *Barbatia ionthados* n. sp. : Holotype. Côte d'Ivoire, Sud Bassam, 200 m, MNHN, 20.6 mm.
8. — *Barbatia legumen* (Lamy) : Angola, Corimba, Luanda province, Praia Etambar, between rocks at low tide, MNHN. 41 mm.
9A-B. — *Barbatia legumen* (Lamy) : Angola, 10 km. S of Ambrizete, Zaire province, intertidal, on beach, MNHN. 24 mm.
10. — *Barbatia legumen* (Lamy) : R.P. Congo, Pointe-Noire, Plage Mondaine, MNHN. 53 mm.

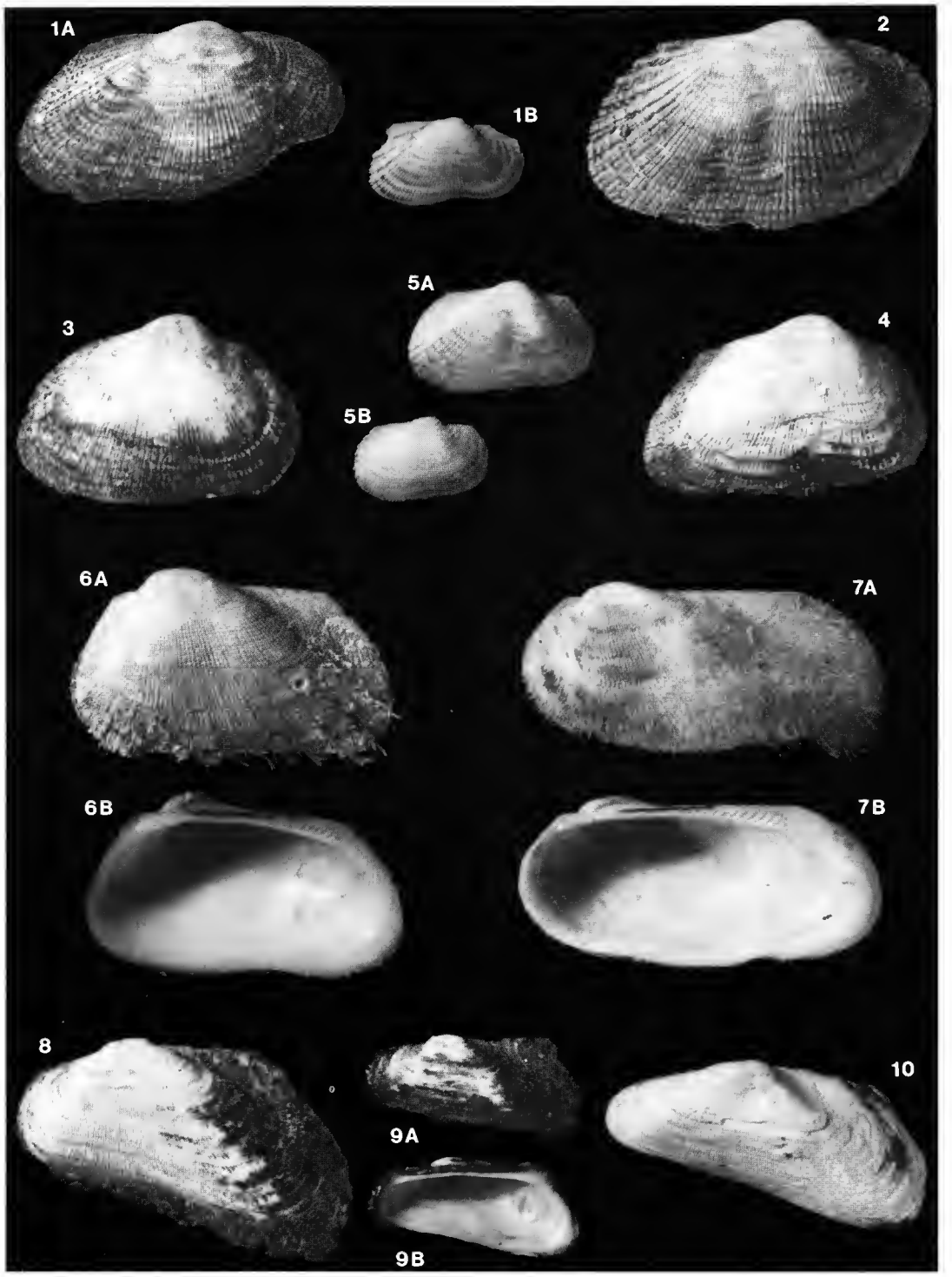

PLATE III

PLATE IV

1A-B. — *Barbatia* (*Nipponarca*) *allocostata* n. sp. : Holotype, Guinea-Bissau : Mouth of Rio Geba, 11°57,5′ N/16°27′ W, 7 m, MNHN. 27.7 mm.
2. — *Barbatia* (*Nipponarca*) *allocostata* n. sp. : Paratype as holotype, MNHN, 28 mm, periostracum removed.
3A-B. — *Anadara geissei* (Dunker) : Angola, Baie de Corimba, Luanda province, 10-20 m, MNHN. 71 mm.
4A-B. — *Anadara geissei* (Dunker) : Angola, Cacuaco, Bengo province, 5-10 m, MNHN. 4A, 33 mm ; 4B, 18 mm.
5. — *Anacara geissei* (Dunker) : Guinea, 9°50′ N/14°14′ W, 15m, MNHN. 52 mm.
6A-B. — *Anadara geissei* (Dunker) : Cape Verde Islands, São Vicente, Baia Porto Grande, on beach, MNHN. 6A, 50 mm ; 6B, 48 mm.

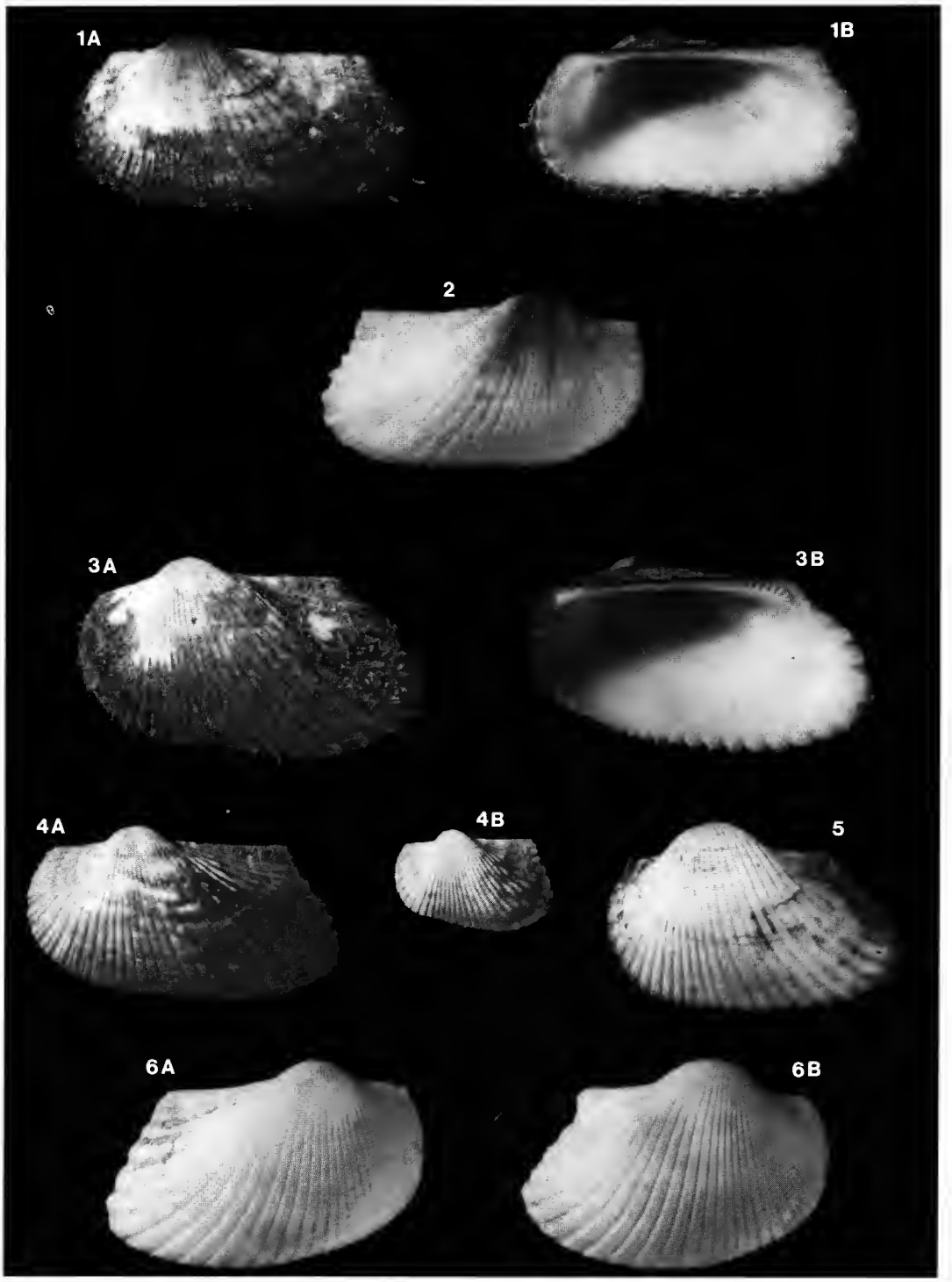

PLATE IV

PLATE V

1A-B. — *Anadara polii* (Mayer) : Mediterranean, Banyuls, MNHN. 34 mm, oblong morph.
2. — *Anadara polii* (Mayer) : Mediterranean, Naples, MNHN. 39 mm, intermediate form.
3A-C. — *Anadara polii* (Mayer) : Atlantic Morocco, MNHN. 3A, 30°24′ N/09°54′ W, 105 m, 28 mm, oblong morph. 3B, 30°26′ N/09°44′ W, 65 m, 23 mm, anteriorly constricted morph. 3C, 30°05′ N/09°50′ W, 110 m, 22 mm, globose morph.
4A-B. — *Anadara polii* (Mayer) : Senegal, 14°50,1′ N/17°29,3′ W, 150 m, MNHN. 4A, 31 mm, oblong morph. 4B, 29 mm, globose morph.
5. — *Anadara polii* (Mayer) : Côte d'Ivoire, 05°01′ N/05 °17′ W, 40 m, MNHN. 24 mm, oblong morph.
6. — *Anadara polii* (Mayer) : Côte d'Ivoire, off Abidjan, 70 m, MNHN. 22 mm, oblong morph.
7. — *Anadara polii* (Mayer) : Senegal, off Dakar, 200 m, MNHN. 24 mm, anteriorly constricted morph.
8. — *Anadara polii* (Mayer) : Cameroon, 02°39′ N/09°40′ E, 60-65 m, MNHN. 26 mm, anteriorly constricted morph.
9. — *Anadari polii* (Mayer) : Gabon, 00°32,8′ N/08°43,1′ E, 125-145 m, MNHN. 39 mm, anteriorly constricted morph.

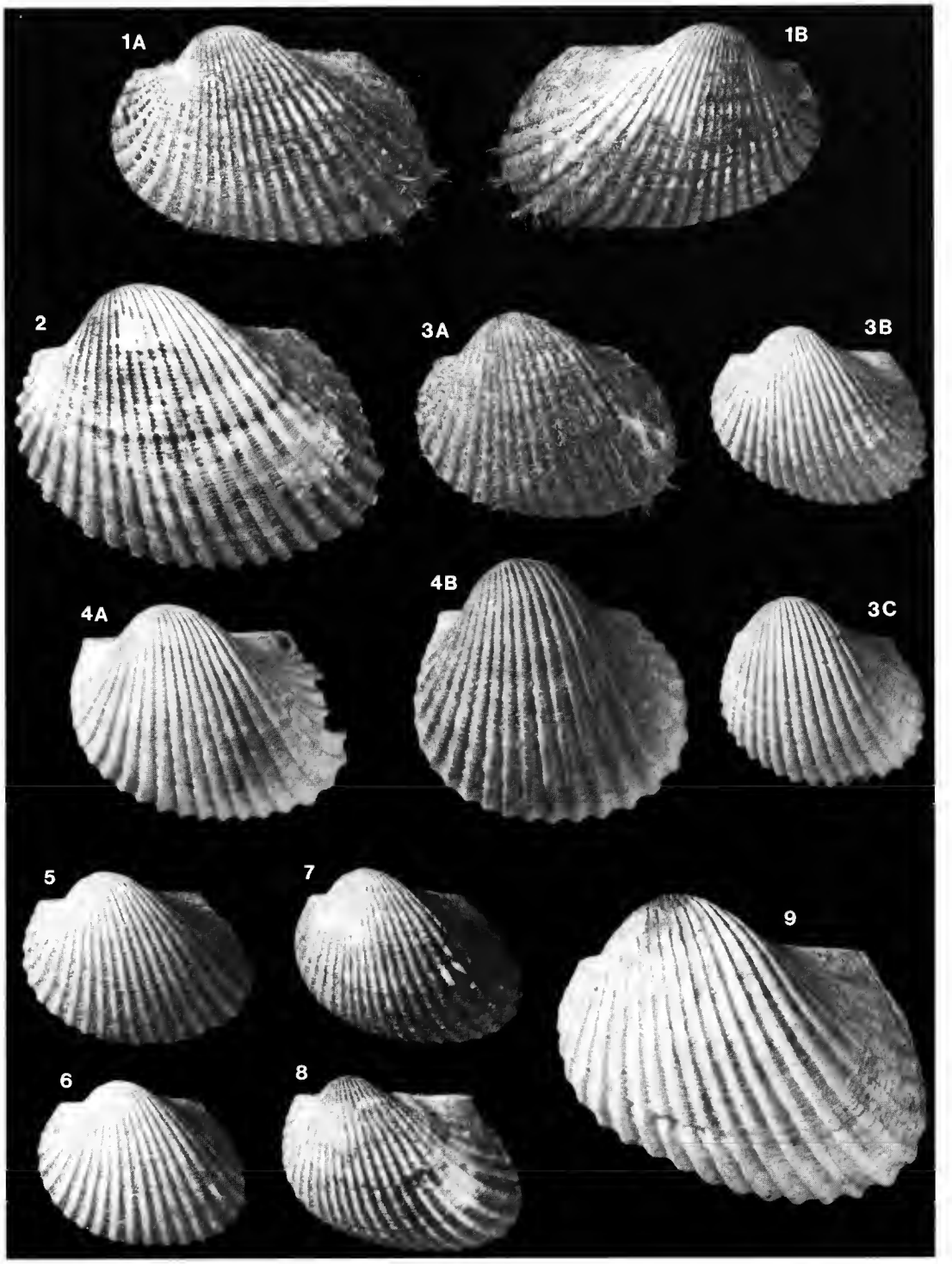

PLATE V

PLATE VI

1A-D. — *Anadara eborensis* n. sp. : Holotype. Côte d'Ivoire, off Grand Bassam, 20 m, MNHN. 31.9 mm.
2A-B. — *Anadara subglobosa* (Dunker) : Mauritania, 17°30′ N/16°15′ W, 100 m, MNHN. 18.5 mm.
3A-D. — *Anadara senegalensis* (Gmelin) : Côte d'Ivoire, off Abidjan, 20 m, MNHN. 3A-C, 21.8 mm. 3D, 23.5 mm.
4A-B. — *Anadara senegalensis* (Gmelin) : Guinea-Bissau, 12°05′ N/17°02,5′ W, 14 m, MNHN. 21.8 mm.
5A-B. — *Anadara senegalensis* (Gmelin) : Angola, Cacuaco, Bengo province, 0-10 m, MNHN. 15.8 mm.
6A-C. — *Anadara camerunensis* n. sp. : Holotype. Cameroon, Victoria/Limbe, 8-10 m, MNHN. 15.1 mm.

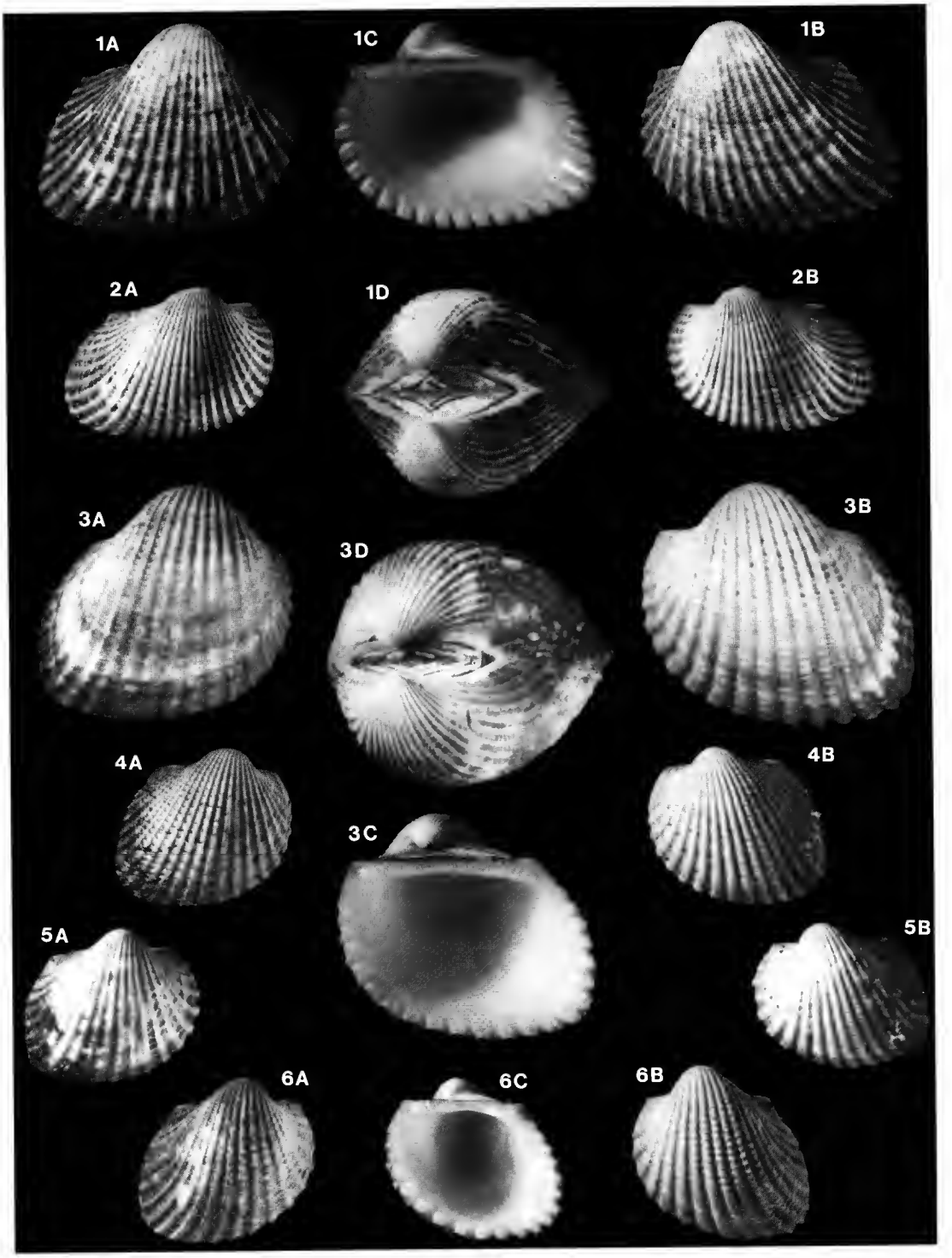

PLATE VI

PLATE VII

1. — *Anadara senegalensis* (Gmelin) : Senegal, South Casamance, Cap Skirring-Diembéring, on beach, MNHN. 23.1 mm.
2. — *Anadara senegalensis* (Gmelin) : Senegal, South Casamance, Cap Skirring-Diembéring, on beach, MNHN. 25.4 mm, Casamance variant.
3. — *Anadara senegalensis* (Gmelin) : Senegal, North Casamance, Abéné-Kafoutine, on beach, MNHN. 23.0 mm, intermediate form.
4. — *Anadara senegalensis* (Gmelin) : Senegal, North Casamance, Abéné-Kafoutine, on beach, MNHN. 26.2 mm, Casamance variant.

5A-D. — *Anadara corbuloides* (Monts.) : Angola, off Ponta das Lagostas, Bengo province. 30-50 m, MNHN. 69 mm.

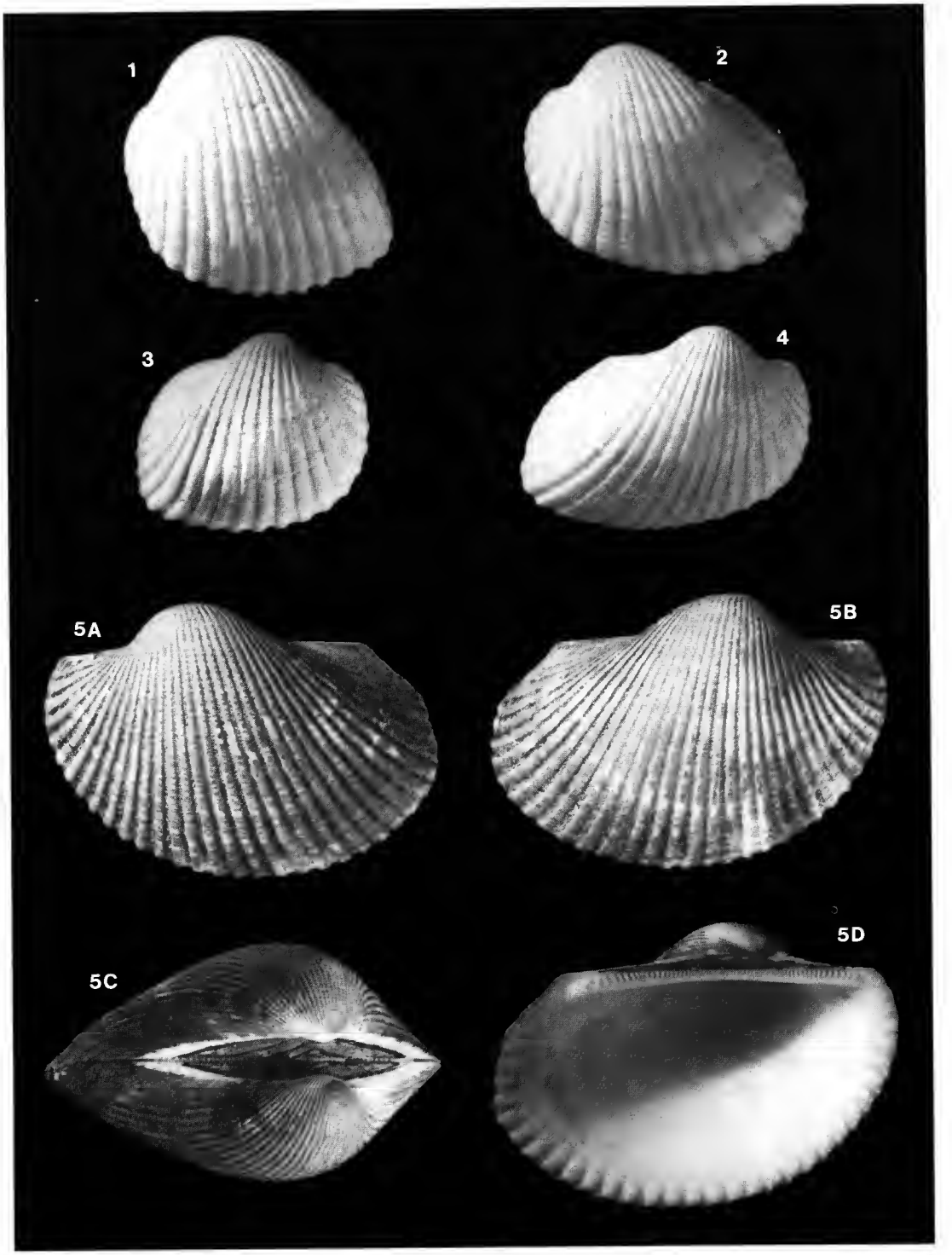

PLATE VII

PLATE VIII

1A-B. — *Senilia senilis* (Linné) : Angola, Cacuaco, Bengo province, MNHN. 92 mm.
2. — *Senilia senilis* (Linné) : Angola, Pta. do Mussulo, Luanda province, MNHN. 50 mm.
3. — *Senilia senilis* (Linné) : Gabon, Cap Esterias, Pointe Idolo, MNHN. 39 mm.
4. — *Bathyarca grenophia* (Risso) : Morocco, 35°35′ N/03°45′ W, 480 m, MNHN. 8.4 mm.
5. — *Bathyarca inaequisculpta* (Smith) : Angola, 14°40′ S/09°54′ E, 3797 m, NMWZ. 6.7 mm.
6A-B. — *Bentharca asperula* (Dall) : Angola, 14°31,8′ S/09°46′ E, 3975 m, NMWZ. 10.7 mm.

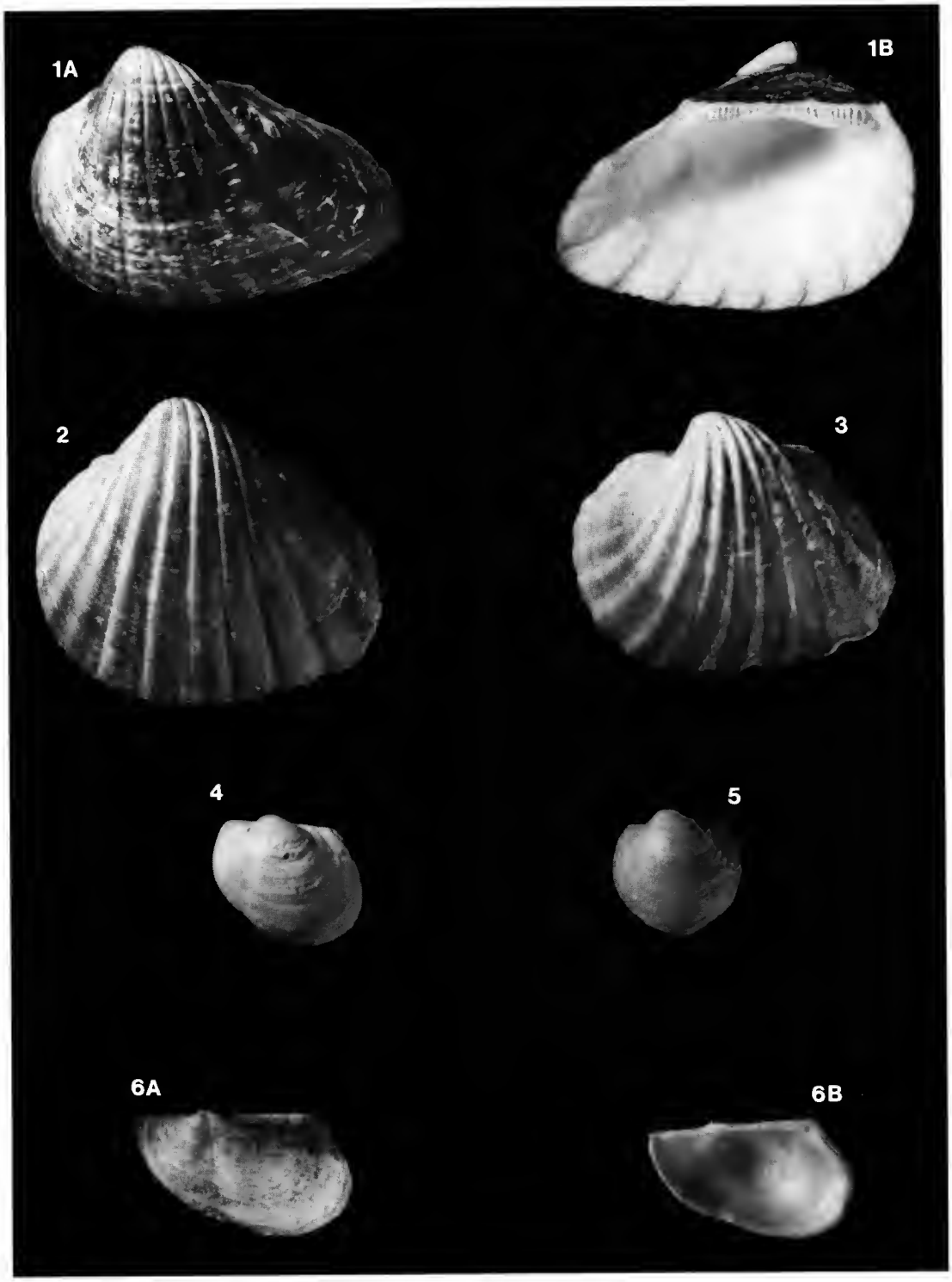

PLATE VIII

PLATE IX

Scanning electron micrographs of the periostracal bristles from the carinal ridge of : A, *Arca avellana turbatrix* n. ssp. and B, *Arca imbricata* (Brug.) from Florida. (Scale bar = 0.5 mm.)

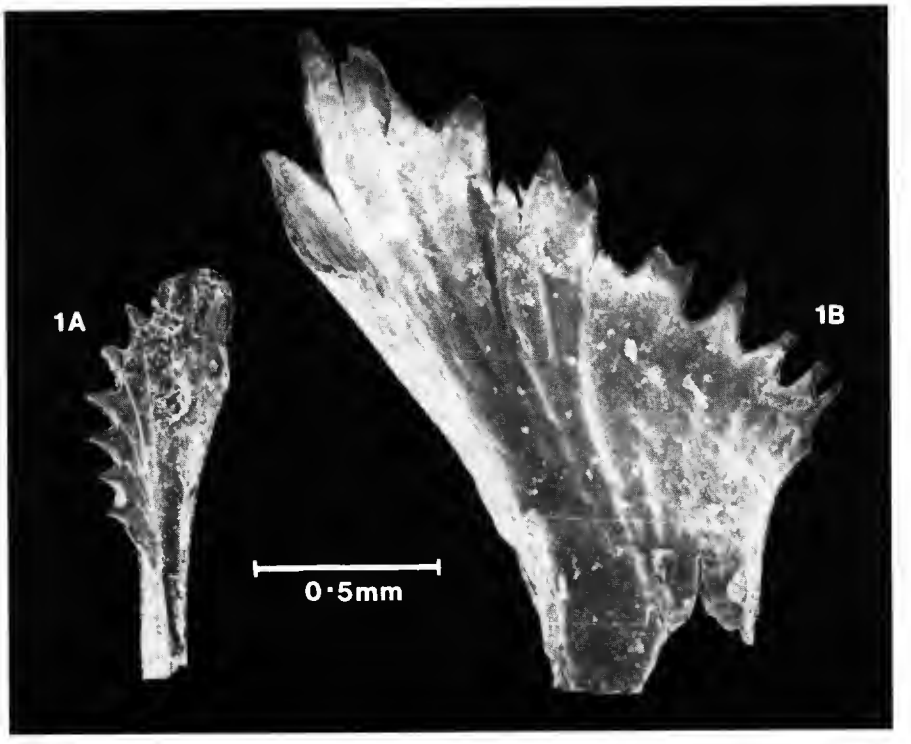

PLATE IX

Bull. Mus. natl. Hist. nat., Paris, 4e sér., **14**, 1992,
section A, nº 2 : 383-404.

El género *Hygromia* Risso, 1826 en la Península Ibérica, con descripción de *Hygromia gofasi* sp. nov., y consideraciones sobre la interpretación funcional del aparato estimulador de Hygromiidae

por Carlos E. Prieto y Ana I. Puente

Resumen. — Una nueva especie de *Hygromia, H. gofasi* sp. nov., se describe de una localidad de Andorra. Sus características anatómicas, intermedias entre los dos subgéneros descritos, no permiten su inclusión en ninguno de ellos. Además, se redescribe *Helix Tassyi* Bourguignat, 1884 a partir del holotipo, que por el momento se considera especie válida de *Hygromia*. Por otra parte, se ha efectuado una revisión bibliográfica de las especies del género en la Península Ibérica, lo que, junto al estudio de numeroso material, ha permitido perfilar sus distribuciones : *H. cinctella* en la región de Montpellier y en Pyrénées-Atlantiques, donde ha sido introducida; *H. limbata*, ampliamente extendida desde el sur de Aude y norte de Barcelona hasta el centro de Cantabria, y hasta la Sierre de la Demanda hacia el interior peninsular; *H. tassyi* en una pequeña región del sur de Ariège. Finalmente, se discuten las dos posibles vías de emisión de la secreción mucosa en *Hygromia* durante la cópula, concluyendo que ésta se produce por el extremo de la estructura vaginal interna, previo almacenamiento en el saco accesorio, lo que invalidaría la hipótesis que considera al saco accesorio como un saco del dardo degenerado. Además, se aportan otros datos que apoyan la hipótesis de la funcionalidad del saco accesorio de Hygromiidae como reservorio de la secreción mucosa.

Résumé. — Une nouvelle espèce du genre *Hygromia, H. gofasi* sp. nov., est décrite d'une localité d'Andorre. Ses caractéristiques anatomiques, intermédiaires entre les deux sous-genres décrits, ne permettent de l'inclure dans aucun d'entre eux. *Helix tassyi* Bourguignat, 1884 est redécrite à partir de l'holotype et considérée comme une espèce valide d'*Hygromia*. Une révision bibliographique des espèces du genre dans la Péninsule Ibérique, ainsi que l'étude d'un abondant matériel ont permis de préciser les distributions : *H. cinctella* dans la région de Montpellier ainsi que dans les Pyrénées-Atlantiques, où elle a été introduite; *H. limbata* très répandue depuis le sud de l'Aude et le nord de Barcelone jusqu'au centre de Cantabria et, vers l'intérieur péninsulaire, jusqu'à la Sierra de la Demanda; *H. tassyi* dans une petite région du sud de l'Ariège. Finalement, les deux voies possibles d'émission de la sécrétion muqueuse pendant la copulation chez *Hygromia* sont discutées. Il est conclu que celle-ci se produit par l'extrémité de la structure vaginale interne, avec au préalable une accumulation dans le sac accessoire, ce qui invaliderait l'hypothèse selon laquelle le sac accessoire serait un sac du dard dégénéré. D'autres données sont apportées à l'appui de l'hypothèse de la fonctionnalité du sac accessoire des Hygromiidae comme réservoir de la sécrétion muqueuse.

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Introducción

La clasificación del género *Hygromia* Risso, 1826 ha sufrido numerosas vicisitudes en los últimos años a causa de las diferentes interpretaciones de las estructuras de valor taxonómico, especialmente del aparato genital. Un resumen de la misma se presenta en Giusti y Manganelli (1987), quienes consideran que *Hygromia* (con los subgéneros *Hygromia* s. str. y *Riedelia*) es un género independiente de *Zenobiella, Lozekia, Ganula* y *Pyrenaearia*, taxones que anteriormente han estado incluidos en *Hygromia*.

Así, *Hygromia* incluiría únicamente dos especies, *Hygromia* (s.str.) *cinctella* (Draparnaud, 1801) e *H. (Riedelia) limbata* (Draparnaud, 1805). Sin embargo, Bourguignat (1884), en uno de sus últimos trabajos, describió la nueva especie *Helix tassyi* de Auzat (Ariège), indicando su pertenencia « au groupe des *Limbata*, groupe composé de formes spéciales à la chaîne des Pyrénées et aux contrées occidentales de la France », y remarcando que « Aucune de ces Hélices ne peut être confondue avec la *Tassyi*, qui est, sans contredit la plus caractérisée et la plus remarquable des formes de ce groupe ». Esas otras formas a que hace referencia Bourguignat (1884) (*odeca* Bourguignat in Locard, 1882, *hylonomia* Bourguignat in Locard, 1882 y *sublimbata* Bourguignat in Locard, 1882) son incluidas entre los sinónimos de *H. limbata* por Germain (1930), quien, no obstante, considera a *Hygromia tassyi* especie válida. La única mención reciente en este sentido es la de Richardson (1980), quien también la incluye entre los taxones válidos de *Hygromia*. Por el contrario, Bofill *et al.* (1918) incluyen en la « forma pirenaica de *H. limbata* » a *H. tassyi*.

No hace mucho tiempo tuvimos ocasión de recolectar en una localidad de Andorra material perteneciente a *Hygromia* pero no asignable a *H. limbata* ni a *H. cinctella*. Dada la escasa distancia entre esta localidad y la típica de *H. tassyi*, referimos en principio tal material a esta última. Sin embargo, una comparación con el holotipo de *H. tassyi* no ha confirmado tal suposición, por lo que el material procedente de Andorra es asignado a un nuevo taxón, *Hygromia gofasi* sp. nov. Además, se redescribe y figura *H. tassyi* a partir del citado holotipo.

Por otra parte, el estudio de material referible a *H. cinctella* procedente del departamento de Pyrénées-Atlantiques, así como otro numeroso para *H. limbata* de diversas localidades peninsulares, ha permitido revisar y actualizar los datos de las especies del género en la Peninsula Ibérica, así como discutir las distintas interpretaciones dadas a las partes del aparato estimulador de *Hygromia*.

Hygromia gofasi sp. nov.

Locus typicus : Santuario de Meritxell (Andorra, CH8412, 1600 m), 24.07.1983, C. E. Prieto y A. G. Prieto leg., 15 ej., bajo piedras esquistosas junto a la fuente del santuario. Holotipo y 12 paratipos en la colección de Malacología de la Universidad del País Vasco ; 2 paratipos en el Muséum national d'Histoire naturelle de Paris.

Descripción

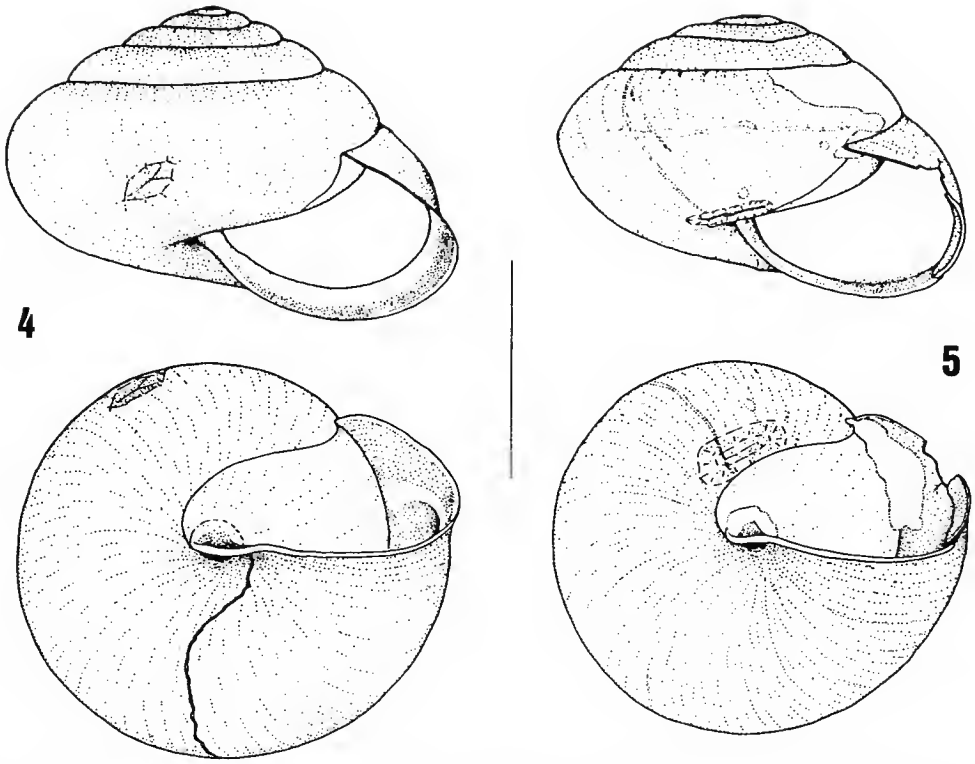
Concha (figs. 2, 4, 6) : Globulosa, convexo-cónica por encima y globosa por debajo ; ombligo casi recubierto ; espira cónica formada por 5.5-6 vueltas convexas de crecimiento

lento; última vuelta poco más ancha que la anteúltima, redondeada y apenas descendente; suturas marcadas; abertura oblicua y ovalar con peristoma blanquecino, frágil, algo reflejado y con un labio interno blanco bien marcado; borde columelar ensanchado y reflejado sobre el ombligo; cáscara delgada, translúcida, de color córneo amarillento, sin banda carenal y frecuentemente con escoriaciones; estriación fina con microescultura a modo de pequeñas escamas.

Dimensiones del holotipo : diámetro = 10.8 mm; altura = 7.6 mm.

FIG. 1-3. — Conchas de las especies de *Hygromia* conocidas anatómicamente. 1, *H. cinctella* (Peyrehorade, Pyrénées-Atlantiques); 2, *H. gofasi* sp. nov. (Meritxell, Andorra); 3, *H. limbata* (Kakouetta, Pyrénées-Atlantiques). Todas, × 2.65.

Aparato genital (figs. 7-12) : Gónada, conducto hermafrodita, glándula de la albúmina y espermoviducto sin especiales características. *Parte masculina* : Conducto deferente largo y delgado. Flagelo corto y puntiagudo (l = 1.5-2 mm). Epifalo muy largo, con grosor uniforme y generalmente enrollado. Músculo retractor del pene largo y delgado. Pene cilíndrico y mitad de largo que el epifalo; está plegado sobre sí mismo por causa de una fuerte vaina conjuntivo-



FIGS. 4-5. — 4, concha de *H. gofasi* sp. nov. (holotipo); 5, concha de *H. tassyi* (holotipo). Escala : 5 mm.

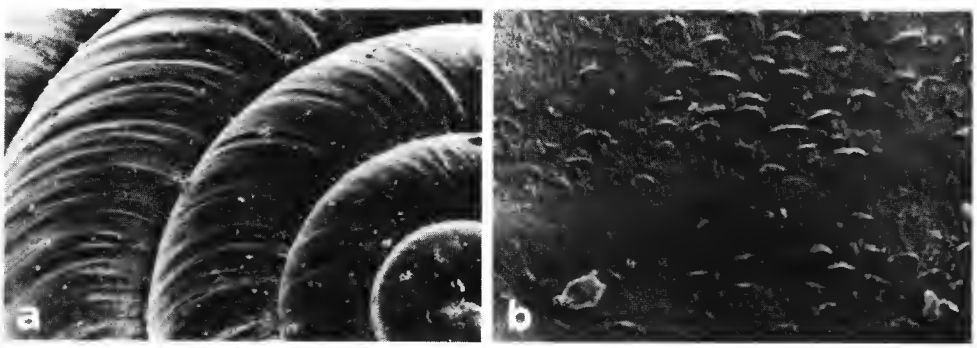
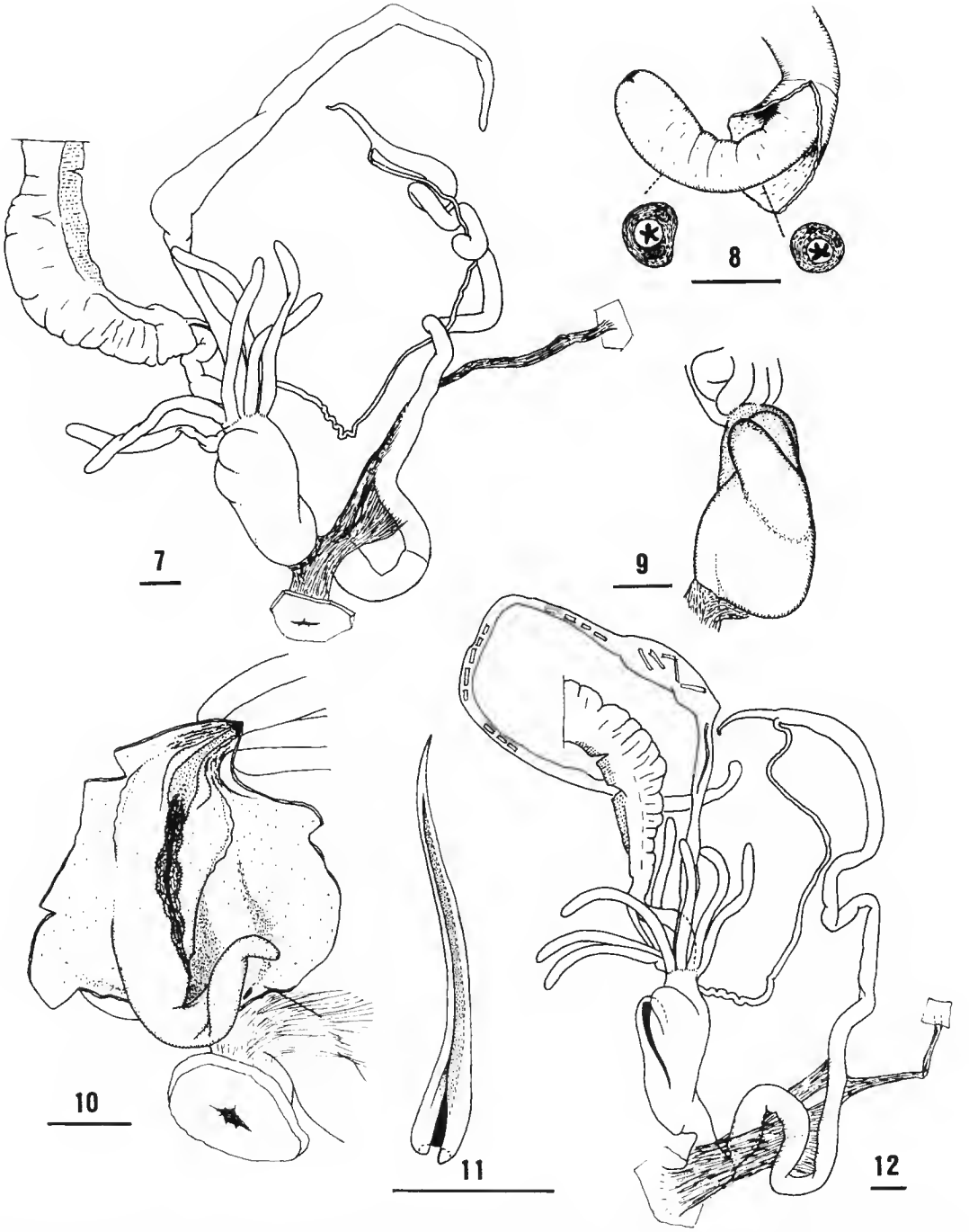


FIG. 6. — Microescultura de la concha de *H. gofasi* sp. nov. (a, × 50; b, × 500).



FIGS. 7-12. — *Hygromia gofasi* sp. nov. : aparato genital y algunas de sus partes (Meritxell, Andorra). 7, parte distal del aparato genital; 8, papila penial y dos secciones transversales a diferentes niveles; 9, vista lateral del complejo del saco del dardo; 10, interior de la vagina mostrando el cono vaginal (holotipo); 11, dardo; 12, parte distal del aparato genital de otro paratipo. Escala : 1 mm.

muscular existente entre la parte proximal del pene y la región atrial. En el interior del tercio distal del pene se encuentra una papila penial cílindrica (fig. 8), de unos 3 mm de longitud y con abertura apical; en sección transversal muestra una pared gruesa con dos pequeñas lagunas y un canal central en forma de estrella. *Parte femenina* : Oviducto libre de mediana longitud, generalmente plegado. De su base parte un conducto tan grueso como el oviducto libre y de mediana longitud que desemboca en una bursa copulatrix muy larga y delgada, con su parte basal más engrosada que la estilizada parte distal. Glándulas mucosas, 6 a 8 que parten de cuatro puntos, dispuestas radialmente alrededor de la parte inicial de la vagina. Vagina corta y muy engrosada, con dos sacos en uno de sus lados, el interno más grueso y corto que el externo, el cual está diferentemente orientado y algo arqueado sobre el interno (fig. 9). El interior de la vagina está ocupado casi totalmente por una estructura alargada, cónica y adosada a la pared de la vagina en el lado donde están situados los sacos (fig. 10); el citado cono vaginal está perforado en su extremo y generalmente doblado sobre sí mismo; en el lado vaginal presenta una larga grieta que, cuando está abierta, muestra numerosos pliegues en sus labios y un profundo surco en el centro, recorrido por un pliegue, donde desembocan los sacos interno (= saco accesorio, carente de dardo) y externo (= saco del dardo), respectivamente en los extremos superior e inferior de la grieta. Este surco, una vez rebasada la salida del saco con dardo, se continúa por un conducto hasta el extremo apical del cono, donde se abre a la vagina. En la parte basal del cono vaginal se aprecia un canal, que se dirige hacia la base de las glándulas mucosas, y numerosos pequeños pliegues. El saco interno, de paredes gruesas y musculosas, está vacío, mientras que el externo presenta un dardo ligeramente retorcido y acanalado en toda su longitud (fig. 11). Finalmente existe un atrio corto.

Rádula : Fórmula 25-26 + C + 25-26. Diente central con una fuerte placa basal, un grueso mesocono y dos minúsculos ectoconos. Primeros dientes laterales con un grueso mesocono y un corto y grueso ectocono. Ultimos laterales con mesocono con una protuberancia en el lado interno. Dientes marginales con mesocono de 2 ó 3 puntas proyectado sobre el ectocono del diente anterior y ectocono dividido de 2 a 5 cúspides irregulares.

Derivatio nominis : La nueva especie está dedicada a Serge Gofas, sin cuya ayuda y valiosas sugerencias no hubiera sido posible la descripción del taxón.

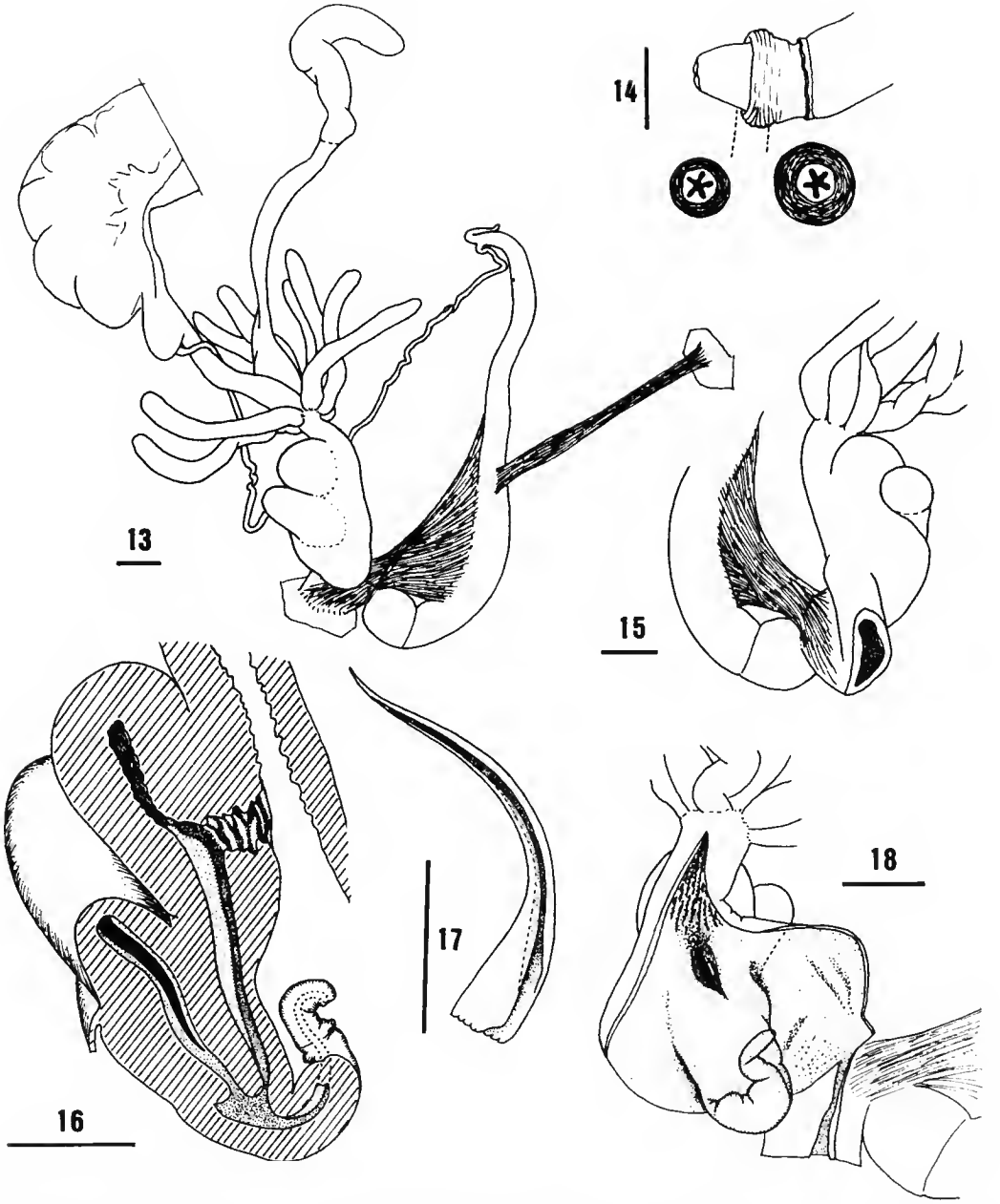
Hygromia tassyi (Bourguignat, 1884)

Helix tassyi Bourguignat, 1884, *Bull. Soc. Malac. France*, 1 : 357.

Locus typicus : « La vallée de Vicdessos, sur les rochers humides des contreforts du pic du Montcalm, au-dessus du Village d'Auzat (Ariège) ». Holotipo en colección Bourguignat, Muséum d'Histoire naturelle de Genève.

Redescripción

Concha (fig. 5) : Pequeña (diámetro = 9.8 mm; altura = 6.4 mm), globosa, algo deprimida, convexo-redondeada por encima, casi aplanada en el ápice, con ombligo muy estrecho y casi totalmente recubierto por el borde columelar; espira formada por 5 1/4 vueltas poco convexas, de crecimiento lento y suturas poco profundas; última vuelta apenas mayor



FIGS. 13-18. — *Hygromia cinctella* : aparato genital y algunas de sus partes (Peyrehorade, Pyrénées-Atlantiques). 13, parte distal del aparato genital; 14, papila penial y dos secciones transversales a diferentes niveles; 15, vista posterior del complejo del saco del dardo; 16, sección longitudinal del complejo del saco del dardo; 17, dardo; 18, interior de la vagina mostrando el cono vaginal. Escala : 1 mm.

que la anteúltima, angulosa al principio, con una banda carenal blanquecina estrecha que desaparece hacia la abertura. Abertura oblícua, ovalada, apenas descendente; peristoma blanquecino, frágil y no engrosado, con el borde columelar reflejado sobre el ombligo. Cáscara frágil, translúcida, de color olivaceo claro, con estriación irregular poco marcada.

Posición sistemática de *Hygromia gofasi* sp. nov. e *H. tassyi*

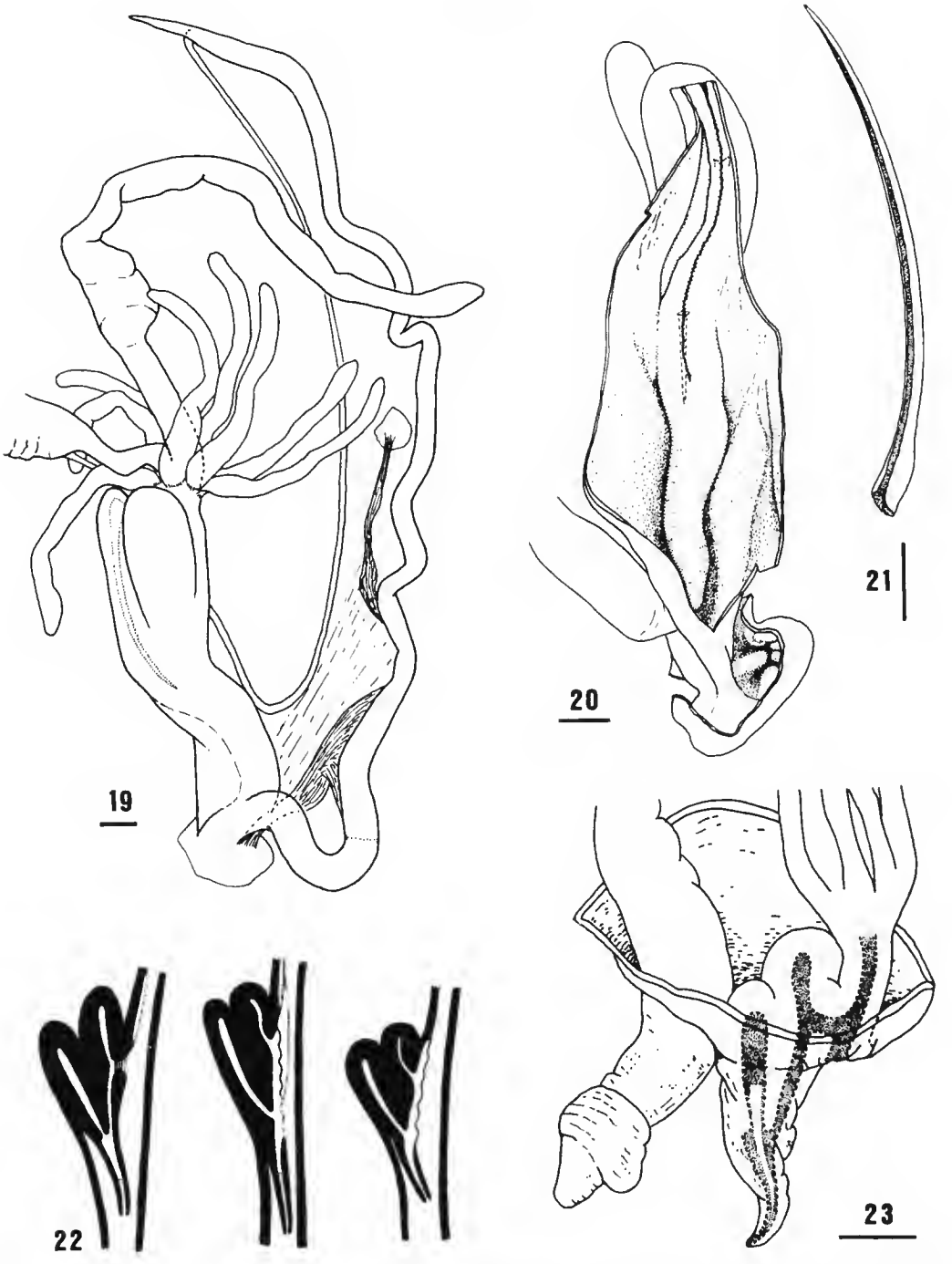
La concha de *H. gofasi* (figs. 2, 4) se diferencia de las otras especies de *Hygromia* (figs. 1, 3, 5) en la falta completa de la banda y de la angulosidad carenal, presente siempre en *H. cinctella*, frecuentemente en *H. limbata* y visible en el holotipo de *H. tassyi*. En común con *H. limbata*, presenta una abertura con peristoma provisto de reborde interno; la microescultura de la concha (fig. 6), formada por crestas muy poco marcadas, parece así mismo más similar a la de *H. limbata* (Giusti y Manganelli, 1987 : pl. 8, figs. C-D). En lo que se refiere al tamaño, *H. gofasi* es notablemente más pequeña que *H. limbata* (diámetro : 12-17 mm, según Germain, 1930), aunque se aproxima a las dimensiones mínimas citadas por Bofill *et al.* (1918) de algunas localidades pirenaicas.

Las peculiaridades conquiológicas de *H. tassyi* la separan de las demás especies del género; no obstante, su validez sistemática queda pendiente hasta que sea posible estudiar anatómicamente ejemplares topotípicos.

Anatómicamente, las diferencias señaladas por Giusti y Manganelli (1987) entre los subgéneros de *Hygromia* parecen claras : En *Hygromia* s. str. (figs. 13-18), el saco del dardo es de tamaño similar al accesorio y está provisto de un dardo retorcido, la bursa copulatrix es oval-alargada con un conducto bastante largo, y el pene y epifalo son de longitud media, mientras que en *Riedelia* (figs. 19-21), el saco del dardo es más esbelto y pequeño que el accesorio y está provisto de un dardo arqueado, la bursa copulatrix es larga y delgada y con conducto bastante corto, y finalmente el pene y epifalo son muy largos y delgados. Además se ha observado en *H. limbata* que el atrio está envuelto por una vaina que en uno de los lados forma una cavidad tapizada por crestas o gruesas papilas (fig. 20), carácter que no ha sido observado en las otras dos especies del género investigadas anatómicamente, y que recuerda a la cavidad o vaina presente en la región atrial de *Monachoides* (Schileyko, 1972, 1978).

Estas diferencias, sin embargo, no son tan marcadas si se tiene en cuenta el aparato genital de *H. gofasi*. Este presenta algunas estructuras que recuerdan a las descritas para *H. cinctella*, especialmente la forma y el tamaño del saco del dardo, curvado sobre el saco accesorio, la forma del dardo, ligeramente retorcido, y finalmente, la posición de los sacos cerca del atrio, mientras que, por el contrario, la estructura de la papila penial, alagarda y con lagunas, y la gran longitud del epifalo respecto del pene, así como la morfología del cono vaginal y de la bursa copulatrix indican una mayor relación con *H. limbata*.

No obstante, varias de las características que relacionan estas dos últimas especies parecen ser plesiomórficas para *Hygromia* : una papila penial larga y cilíndrica la presentan numerosos géneros de Hygromiinae, mientras que una abertura larga en el cono vaginal (fig. 22), un dardo con aristas desarrolladas y una bursa copulatrix alargada con un conducto corto aparecen también en *Zenobiella* (Giusti y Manganelli, 1987) ; por el contrario, parecen ser características apomórficas del género el corto flagelo frente a un epifalo muy largo y la acanaladura a lo largo del dardo, originada posiblemente a partir de un ensanchamiento de



FIGS. 19-23. — 19-21, *Hygronia limbata* : 19, aparato genital (Monte Altxueta, Navarra); 20, interior de la vagina mostrando el cono vaginal y la vaina atrial (Kakouetta, Pyrénées-Atlantiques); 21, dardo (como la fig. 19); 22, secciones esquemáticas longitudinales de la vagina mostrando la relación entre los sacos y las estructuras vaginales : izquierda, *H. cinctella*, centro, *H. limbata*, derecha, *Zenobiella subrufescens* (modificado de GIUSTI y MANGANELLI, 1987); 23, partes evertidas del aparato genital de *H. cinctella* mostrando la posición de los conductos internos del aparato estimulador (modificado de GIUSTI y MANGANELLI, 1987). Escala : 1 mm.

dos aristas de las cuatro existentes en el dardo de *Zenobiella*. *H. gofasi* se encontraría en una posición intermedia entre *Hygromia* s. str. y *Riedelia*, por lo que cabe preguntarse hasta qué punto tiene sentido la diferenciación subgenérica.

Por otra parte, y al margen de lo anterior, la morfología angulosa de la concha y la falta de peristoma en *H. cinctella* recuerdan a ejemplares juveniles de *H. limbata*, como lo atestiguan las determinaciones erróneas de *H. cinctella* que se comentan en el siguiente apartado; igualmente, el largo conducto de la bursa copulatrix y la reducida longitud de la parte masculina, en comparación con los de *H. limbata*, parecen indicar un origen de *H. cinctella* a partir de individuos no adultos de una especie ancestral de *Hygromia* que hubiesen alcanzado prematuramente la madurez sexual. En este sentido, GOULD (1977 : figs. 47-48) presenta la formación iterativa de morfos carenados originados por pedogénesis en *Poecilozonites bermudensis* en la que, al igual que en *H. limbata*, las conchas juveniles son carenadas mientras que las adultas sólamente angulosas.

REVISIÓN BIBLIOGRÁFICA DE LAS ESPECIES DE *Hygromia* EN LA PENÍNSULA IBÉRICA

Las citas referida a *Hygromia cinctella* del sur de Francia y noreste de España son numerosas, pero la mayoría son menciones genéricas y no recogidas aquí; las localidades concretas son muy escasas, y parte deben ser consideradas erróneas :

FAGOT (1880) indica que gran parte de las determinaciones realizadas por MERMET (1843) son erróneas y, en concreto, señala que la cita de *H. cinctella* de Parc de Pau (YN19) debe referirse a conchas juveniles de *H. limbata*, indicando lo mismo para las de NANSOUTY (1872), quien la citó de Hendaye (XP00) y Cambo-les-Bains (XP20); GERMAIN (1930) parece seguir este criterio, ya que no menciona la presencia de *H. cinctella* en el departamento de Pyrénées-Atlantiques. Sin embargo, WATSON (1919) refiere material de Ciboure (XP10) a *H. cinctella*, presentando figuras de la concha y del aparato genital que confirman su identificación y, también, en cierto modo, las localidades citadas por NANSOUTY (1872), situadas a muy escasa distancia y que, por este motivo, consideramos válidas.

Por otra parte, VILELLA (1965) cita *H. cinctella* de Areo (CH61), en el Pirineo de Lérida, pero no *H. limbata*, especie profusamente citada de dicha región por BOFILL y HAAS (1920*a*); en este sentido, HAAS (1929) refiere a *H. limbata* la cita de *H. cinctella* de GRAELLS (1846) para « Alta Cataluña ». El examen de una concha de las recogidas por VILELLA (1965) muestra una microescultura típica de *H. limbata*, por lo que la hemos referido a esta especie. En cuanto a la cita de *H. cinctella* (LARRAZ y CAMPOY, 1980 ; LARRAZ *et al.*, 1981) de Quinto Real (Navarra, XN26), no es mencionada posteriormente por LARRAZ y JORDANA (1984), quienes indirectamente la consideran referida a *H. limbata*.

Por último, citan *H. cinctella* ANDRÉ (1982, fig. 1 : Ganges : 3 km W, EJ56; Arboras : les Frigoules, EJ34; Laroque, EJ56; Le Claux, EJ45; Cambo, EJ67; La Cadière, EJ66) y PERJESI (1985 : Montpellier, EJ73).

En lo que respecta a *H. limbata* (ver Anexo I), sólamente hemos encontrado dos citas erróneas : el material citado como tal por OJEA y ANADON (1983) del Monte Naranco (Asturias, TP60), una vez examinado, ha resultado ser *Mengoana brigantina* (Da Silva Mengo,

1867); por otro lado, BOFILL y HAAS (1920*b*) comentan que la localidad de Vallvidrera (DF38), de la colección Salvañá, debe ser considerada un error de catalogación.

Respecto a *Helix tassyi*, como ya se ha comentado, fue considerada un sinónimo de *H. limbata* por BOFILL *et al.* (1918) pero no por GERMAIN (1930), quien, basándose en la descripción original, la consideró una especie válida. Las localidades citadas por LOCARD (1894) y GERMAIN (1930) no son mas que repeticiones más o menos completas de la original (CH72), pero FAGOT (1890) añade otras dos : « Entre la cascade de l'Arse et le port de Guillou » y « Vallée d'Aulus », ambas en CH63.

DISTRIBUCIÓN GEOGRÁFICA DE LAS ESPECIES DEL GÉNERO *Hygromia*

— *H. gofasi* (fig. 24)

Conocida hasta ahora únicamente de la localidad típica, en Andorra.

— *H. tassyi* (fig. 24)

Conocida hasta ahora de la localidad típica y de otras dos cercanas situadas al noroeste, todas por encima de los 1500 m, en Ariège.

— *H. cinctella* (fig. 24)

NUEVAS LOCALIDADES : Peyrehorade (XP52, 80 m), 14.X.87, C. E. PRIETO y R. MARTIN leg., 8 ej + 1 c; sobre zarzas y ortigas junto riachuelo.

Su área de distribución comprende (GIUSTI y MANGANELLI, 1987) la Peninsula Itálica, Córcega, Archipiélago Toscano, Sicilia y posiblemente Cerdeña, de donde es citada por PERJESI (1985), adamás del sureste de Francia (GERMAIN, 1930; KERNEY *et al.*, 1983). También se encuentra en Viena (Austria), Torquay (Devon, Inglaterra), Dinard (Ille-et-Vilaine) y Budapest (BIGGS, 1958; KERNEY *et al.*, 1983; PERJESI, 1985) como introducciones.

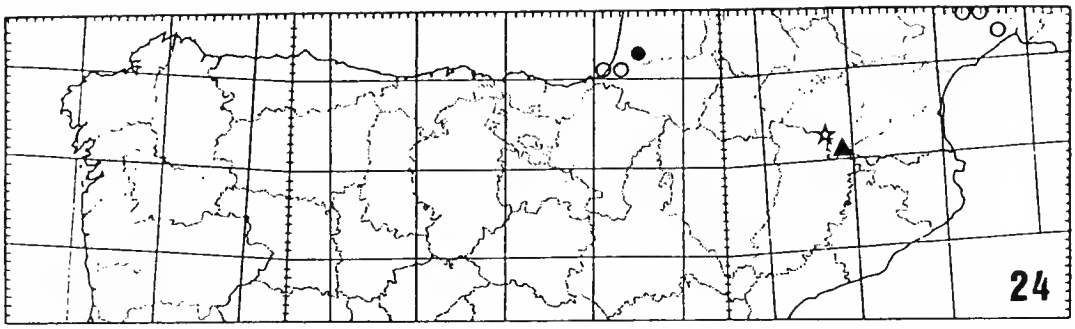
En la zona de estudio presenta una distribución fragmentada en dos subáreas. De un lado, la región de Montpellier, continua con el área principal de distribución (sureste de Francia e Italia), y de otro las localidades citadas de Pyrénées-Atlantiques, las cuales parecen deberse a una próspera introducción. Según GIUSTI y MANGANELLI (1987), esta especie suele encontrarse en áreas húmedas fuertemente humanizadas, lo que indica una susceptibilidad al transporte pasivo, como lo apunta también su presencia en Budapest (PERJESI, 1985) y otras localidades. BIGGS (1958) sugiere que, de acuerdo con los datos de MOQUIN-TANDON (1855), podría haberse extendido por el oeste de Francia durante el siglo pasado.

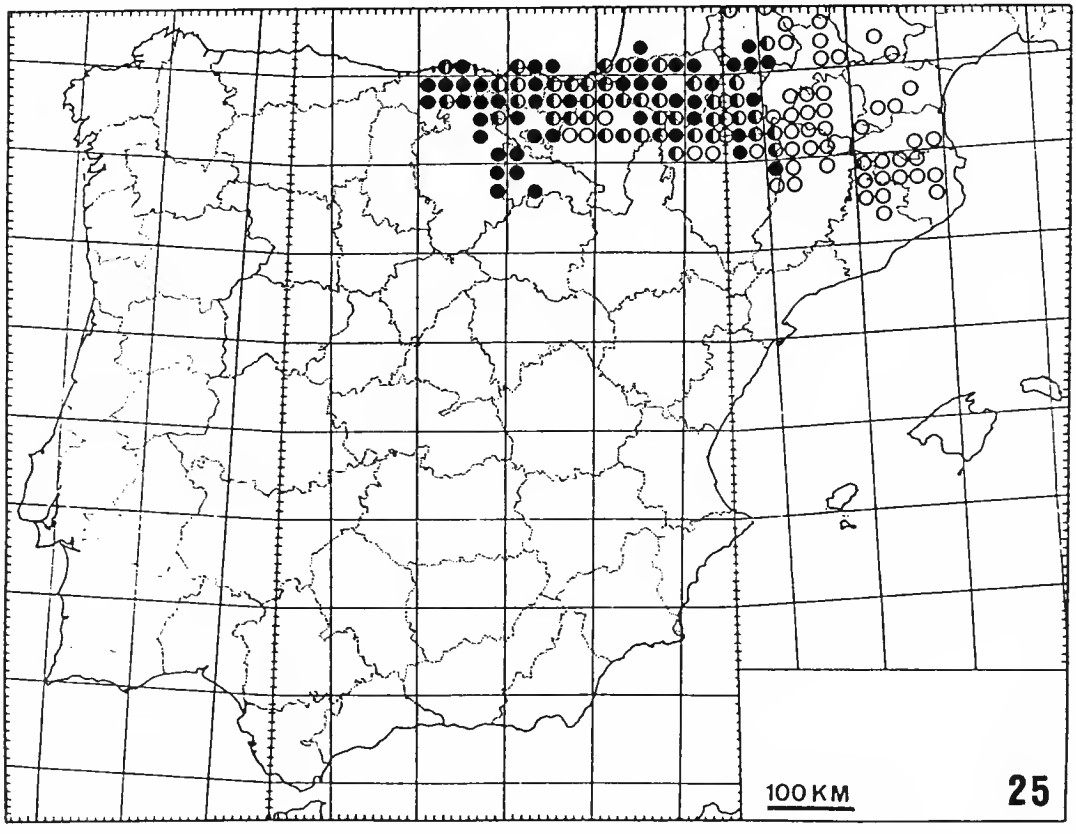
— *H. limbata* (fig. 25)

NUEVAS LOCALIDADES : Ver Anexo II.

Su área de distribución comprende desde el noroeste de Francia (salvo la región de Bretaña) hasta el norte de la Península Ibérica y algunas escasas localidades en el sur de Inglaterra, donde, al parecer, ha sido introducida (GERMAIN, 1930; KERNEY *et al.*, 1983; PRIETO, 1986).

En el área estudiada presenta una distribución muy nítida : región pirenaica y





FIGS. 24-25. — Areas de distribución en la Peninsula Ibérica y S de Francia de las especies de *Hygromia*, sobre cuadriculas UTM con puntos de 20 km de lado. 24, *H. gofasi* sp. nov. (triángulo), *H. tassyi* (estrella) e *H. cinctella* (círculos); 25, *H. limbata*. Los símbolos vacíos indican localidades bibliográficas, los llenos nuevas localidades y los medio llenos, localidades bibliográficas y propias.

subpirenaica y Montes Vascos, desde el norte de Gerona hasta el centro de Cantabria. La depresión del Ebro parece constituir el limite sur de distribución de esta especie, ligada a bosques húmedos. Las nuevas localidades confirman los datos previos y permiten precisar algo más su distribución. Así, *H. limbata* aparece de forma continua en el norte peninsular, desapareciendo paulatinamente hacia el oeste en la región central de Cantabria, donde parece ser sustituida por *M. brigantina*. También falta del centro y este de Burgos, así como de la mitad sur de Alava y Navarra, salvo por su presencia en algunas localidades aisladas situadas en lugares altos como las sierras de Cantabria y de Codés en Alava y Navarra; las localidades riojanas, en la Sierra de la Demanda, podrían constituir un enclave aislado. En Huesca, según material propio, *H. limbata* ocupa únicamente localidades de altitud superior a los 1000 m, y hacia el este se restringe igualmente a las áreas montañosas faltando en el valle del Segre y en el litoral catalán. En Cataluña penetra hacia el sur siguiendo las estribaciones de la Sierra de Montseny.

En la vertiente francesa de Pirineos parece una especie muy común; más al norte disminuye la densidad de localidades (con falta completa de datos para Landes y mitad occidental de Gers); en el extremo oriental de Pirineos, penetra hacia Aude hasta los Montes Corbières, faltando al norte (región de Carcassonne) y al sur (Canigou y valle del Tech). Una actualización de la información corológica con recolecciones intensivas parece urgente, ya que la mayor parte de las localidades del sur de Francia fueron citadas el siglo pasado.

Implicaciones funcionales del aparato estimulador de *Hygromia*

En *H. cinctella*, el saco interno (= saco accesorio) desemboca en la parte basal interna de un cono vaginal (fig. 16), frente a una abertura alargada que se abre al conducto vaginal, cuyas paredes presentan numerosos pequeños pliegues que llegan hasta la desembocadura de las glándulas mucosas (fig. 18); por otra parte, el saco externo (= saco del dardo) desemboca en el interior de la parte media del cono vaginal, donde no hay otra abertura. En *H. limbata* y *H. gofasi* la abertura es tan larga que sobrepasa el punto de desembocadura del saco del dardo (figs. 10 y 20), pero funcionalmente es similar, ya que se encuentra tan fuertemente cerrada en su parte inferior que a menudo resulta indistinguible su presencia.

Durante la cópula, el cono vaginal es evaginado al exterior junto con la papila penial (Giusti y Manganelli, 1987) y el aparato estimulador puede entonces proyectar el dardo (fig. 23). En este proceso, y dada la configuración del aparato estimulador, la secreción de las glándulas mucosas se puede expulsar por una de las dos vías posibles. La primera discurre por la luz vaginal, y la secreción saldría al exterior junto a la base del cono vaginal, es decir, por donde va a ser introducido el espermatóforo. La segunda discurre por el interior del cono vaginal, a través de la abertura situada en su base, con salida por el orificio apical del cono vaginal. Esto supone una vía indirecta más elaborada ya que la secreción mucosa debería producirse antes de la cópula, ser conducida al interior del cono vaginal, almacenada en el saco interno y finalmente proyectada al exterior, junto al dardo, por contracción de la musculatura de los sacos.

Varios hechos inducen a considerar esta segunda vía como más probable :

1. La secreción de las glándulas mucosas se comporta como una feromona, teniendo que entrar en el sistema circulatorio del otro individuo, mediante el pinchazo del dardo como

vector, para que funcione como acortador (activador) de la cópula (ADAMO y CHASE, 1990). En el caso de *Hygromia*, la inyección de la secreción mucosa debe realizarse o bien por la acanaladura presente en el dardo o, si no, debe depositarse lo más cerca posible de los pinchazos producidos por el dardo; en cualquiera de los casos, la secreción debe pasar al conducto interno del cono vaginal antes de la cópula. La secreción mucosa no parece intervenir en la transferencia del espermatóforo (ADAMO y CHASE, 1990); efectivamente, la cópula y la consiguiente transferencia del espermatóforo ocurren siempre, independientemente de la estructura y composición del aparato estimulador. Por tanto, debe desecharse la emisión directa de la secreción mucosa por la luz vaginal en los géneros que presentan cono vaginal. En relación con esto, las glándulas mucosas persisten en grupos que han perdido el saco o los sacos del dardo, pero no existen, sin embargo, géneros con sacos del dardo que carezcan de glándulas anexas (salvo *Circassina circassica* (Mousson, 1863), según SCHILEYKO (1991 : 190)). La aplicación tópica del mucus, como indica CHUNG (1986, en ADAMO y CHASE, 1990) para *Helix*, no tiene efecto en la eversión del genital por lo que, en los grupos sin saco del dardo, la secreción mucosa debe tener otros mecanismos de actuación.

2. La abertura basal del cono vaginal y el conducto existente entre la desembocadura de los sacos carecerían de función si la secreción glandular discurriese directamente por la luz vaginal. Igualmente, el gran tamaño y la fuerte musculatura del saco accesorio indican que se trata de un órgano funcional; en este sentido, no parece lógica la gran variabilidad existente en la forma, tamaño y posición del saco accesorio si se tratase de una estructura residual no funcional, como sugieren GIUSTI y MANGANELLI (1989). Sería interesante la investigación de la composición histoquímica de las sustancias no consolidadas que se suelen observar en el interior del saco accesorio tras su disección, para confirmar su origen en las glándulas mucosas.

3. Los pliegues de la parte superior de la vagina, entre la desembocadura de las glándulas mucosas y la abertura basal del cono vaginal, donde también están presentes, parecen estructuras destinadas a conducir las secreciones mucosas hasta el saco accesorio. Dichos pliegues se encuentran también en géneros carentes de cono vaginal, y discurren entre la inserción de las glándulas mucosas y la desembocadura de los sacos.

IMPLICACIONES SISTEMÁTICAS

En relación con lo expuesto se encuentra el debate actualmente existente sobre la interpretación de las estructuras que forman el aparato estimulador de la familia Hygromiidae, en el que se mantienen dos opiniones claramente enfrentadas, con diferentes implicaciones filogenéticas y sistemáticas.

La posición clásica (GERMAIN, 1930; HESSE, 1931) considera que el saco interno, cuando existen dos en el mismo lado de la vagina, es un saco del dardo residual. Más recientemente, SCHILEYKO (1978, 1991) y GIUSTI y MANGANELLI (1987, 1989), siguiendo esta interpretación, consideran que cuatro sacos del dardo, dos a cada lado de la vagina y provistos de dardos, constituyen el estado plesiomórfico del aparato estimulador de Hygromiidae, y que, tempranamente, los sacos del dardo internos perdieron su funcionalidad quedando como sacos residuales; de esta estructura se derivarían los diferentes aparatos estimuladores presentes en

las subfamilias actuales. Como consecuencia, y utilizando también otros caracteres, SCHILEYKO (1978) considera la superfamilia Hygromioidea (con Hygromiidae únicamente) independiente de Helicoidea (con Helicidae, Bradybaenidae y otras), cuyo aparato estimulador primitivo tendría una estructura radial múltiple, de Sphincterochiloidea, con un primitivo aparato estimulador con sarcobelum, y de Helicodontoidea, con aparato estimulador compuesto por un pequeño saco sin dardo situado en la base de la glándula mucosa única.

La otra posición es más reciente y ha sido propuesta y desarrollada por NORDSIECK (1987), quien considera que el aparato estimulador plesiomórfico de Hygromiidae estaría constituido por dos sacos del dardo, uno a cada lado de la vagina, con sus correspondientes sacos accesorios y haces de glándulas mucosas en posición superior; los sacos accesorios tendrían una función de acumulación de la secreción de las glándulas mucosas y de la subsecuente eyección durante la cópula. Dicho autor considera que Hygromiidae forma un grupo monofilético con Helicidae y Bradybaenidae y que la superfamilia Helicoidea comprende, además de las citadas, a Xanthonychidae y Sphincterochilidae.

En nuestra opinión, la hipótesis elaborada por SCHILEYKO (1978, 1991), carece de pruebas que la avalen puestos que aún no se ha descrito ninguna especie de Hygromiidae con dos pares de sacos provistos de dardos, y porque los sacos carentes de dardo, caso de estar presentes, nunca se encuentran en la posición inferior. La explicación dada por SCHILEYKO (1991 : 190) a estas objeciones no nos parece tan obvia. La segunda hipótesis, por el contrario, puede sustentarse en otros datos :

1. La emisión de la secreción mucosa se efectúa de diversas formas en las familias mencionadas, pero siempre ocurre junto al punto de actuación del dardo o del sarcobelo : en Sphincterochilidae desemboca en la base del apéndice situado en el extremo apical del aparato estimulador atrial (FORCART, 1972); en Xanthonychidae parece haber gran variabilidad (NORDSIECK, 1987), con glándulas desembocando tanto sobre el saco del dardo (*Helminthoglypta, Cepolis*) como en su base (*Trichodiscina, Xanthonyx*); en Bradybaenidae desemboca directamente en un reservorio comunicado e implantado sobre el saco del dardo (SCHILEYKO, 1978; NORDSIECK, 1987); finalmente, en Helicidae, las glándulas presentan troncos musculosos y desembocan directamente en la base del saco del dardo, donde la secreción es conducida inmediatamente por el dardo (ADAMO y CHASE, 1990).

2. En la familia Hygromiidae, las glándulas mucosas desembocan generalmente en la vagina, pero existen algunas exceptiones : en *Ponentina*, género de posición sistemática incierta y que podría constituir una subfamilia propia, como propone SCHILEYKO (1991), desembocan en los sacos accesorios; en *Caracollina*, perteneciente según NORDSIECK (1987) a la subfamilia Ciliellinae, la única glándula mucosa está implantada sobre la vagina, pero está comunicada, mediante un conducto que discurre por la pared de la vagina, con un largo apéndice (= saco accesorio) insertado en el saco del dardo (PRIETO *et al.*, en prensa). Finalmente, y como ya se ha visto, en *Hygromia* se da una relación funcional del saco accesorio con las glándulas mucosas. Se aprecia, por tanto, una amplia variabilidad en la estructura del saco accesorio, de difícil explicación si se tratase de un órgano residual carente de función.

3. En la subfamilia Cochlicellinae (Hygromiidae) no existen sacos con dardo ni glándulas mucosas sobre la vagina; el aparato estimulador es un largo apéndice, ramificado en *Cochlicella barbara* (L., 1758), formado por un tronco grueso y por una región glandular situada en su ápice. De acuerdo con los datos anteriores, este apéndice no sería mas que un

saco accesorio muy modificado sobre el que se insertan una o varias glándulas mucosas. Recientemente, SCHILEYKO (1991) considera que *Cochlicella* pertenece a una familia independiente dentro de Helicoidea.

4. Tampoco existen sacos con dardo en la tribu Monachini (Monachinae), presentando apéndices y glándulas mucosas, con pérdidas de diverso grado; una excepción podría ser *Monacha cartusiana* (O. F. Müller, 1774), donde GIUSTI y MANGANELLI (1987) describen un apéndice inferior (= saco externo degenerado y sin dardo) y un diverticulo superior sacciforme (= saco interno o accesorio). La situación es diferente en la tribu Euomphaliini (Monachinae), donde no existen sacos del dardo pero sí unas largas estructuras vaginales que han sido consideradas tradicionalmente sacos del dardo degenerados : las glándulas mucosas desembocan directamente sobre la vagina y a cierta distancia de estos apéndices.

En conclusión, es dificilmente asumible en nuestra opinión que los sacos accesorios (o sacos internos) sean sacos del dardo degenerados ya que presentan una función bien definida, la de almacenar, y evacuar durante la cópula, la secreción producida en las glándulas mucosas.

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ANEXO I

Recopilación bibliográfica para *Hygromia* (*Riedelia*) *limbata* (Drap., 1805)

METODOLOGÍA : Se han recogido únicamente los trabajos con citas lo suficientemente concretas como para poder ser representadas en coordenadas UTM; todas las restantes (países, provincias o departamentos) han sido omitidas. Sólamente se indica el epíteto específico cuando este difiere del actualmente válido. En cada localidad se indica entre paréntesis el departamento o provincia y sus coordenadas UTM. Para las provincias españolas se utilizan las letras de las matrículas provinciales y para los departamentos franceses las siguientes : AR, Ariège; AU, Aude; GS, Gers; HG, Haute-Garonne; HP, Hautes-Pyrénées; PA, Pyrénées-Atlantiques; PO, Pyrénées-Orientales; TN, Tarn.

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ANEXO II

Lista de localidades de *Hygromia* (*Riedelia*) *limbata* (Drap., 1805)

Las fechas de recolección, los recolectores y el material recogido se han omitido y las coordenadas UTM se han abreviado. Todo el material estudiado se encuentra en la colección de Malacología de la UPV/EHU.

Alava : Altube, WN15; Angosto, VN94; Añés, VN86; Aramayona : Ibarra, WN36; Atauri, WN43; Bajauri, WN32; Délica : cañón río Nervión, WN05; Fuente Los Chorros, WN23; Gurendes, VN94; Ibarra/Mondragón : 2 km, WN36; Murguía : río Bayas, WN15; Orduña : Pico del Fraile, VN95; Osma : Valderoño, VN94; Ribera, VN84; Santa Cruz de Campezo, WN52; Sarría : puente Blanco, WN15;

Sierra Salvada, VN96; Subijana : desfiladero, WN04; Valderejo, VN84; Zárate, WN15. **Burgos** : Bárcenas, VN57; Espinosa de los Monteros, VN56; Estacas de Trueba, VN47; Hayal de Santiago, WN05; Horadada, La : sedim.?, VN63; Mercadillo de Mena, VN77; Montes de Orduña : Txarlazo, VN95; Peña de Orduña, VN95; Quintana Entrepreñas : sedim, VN74; San Zadornil, VN84; Siones, VN76; Villabasil, VN76; Villafría, VN84; Villalba de Losa : Txolope, VN95; Villasana de Mena, VN77; Villasante de Montija/Colina, VN66. **Cantabria** : Agüera, VN79; Alceda, VN28; Arredondo, VN59; Bustablado, VN49; Cotillo, VN18; Entrambasaguas, VP40; Hazas/Asón, VN58; Isla, VP51; Llaguno, VN79; Peña Cabarga, VP30; Puente Viesgo, VN29; Pujayo, VN17; San Román, VP31; Sel de la Peña, VN27; Sierra de Ibío, VN09; Valle Asón, VN58; Vega de Pas : Candolías, VN37; Villacarriedo, VN38. Gers : Beaulieu, CJ03; Masseube/Auch, CJ01; Miélan/Tillac, BJ81; Mirande, BJ92. **Guipúzcoa** : Aitzgorri : 2 km S, WN55; Aitzgorri : Campa de Urbía, WN55; Aizarna : 3 km, WN68; Albistur, WN77; Alkiza, WN78; Alto de Itziar, WN59; Aralar : Oidui, WN76; Arantzazu, WN45; Aritzalde, WN55; Arzallus, WN68; Ataun : San Martín, WN66; Bedayo, WN76; Bengoetxea, WN56; Cerain, WN56; Cestona, WN68; Hernialde, WN77; Motrico, WN59; Ojarbi, WN66; Oñate, WN46; Otzaurte, WN57; Peña Madariaga, WN58; Régil, WN67; San Miguel de Artadi, WN69; San Sebastián : Urgull, Alza y Gladys Enea, WN89; Tolosa, WN77. **Haute-Garonne** : Astau, BH93; Superbagnères, CH03. **Hautes-Pyrénées** : Bagnères-de-Bigorre/Gerde, BH67; Bareilles, BH95; Betpouey, BH55; Cadéac/Gouaux, BH85; Cauterets : N, YN35; Ost, YN36; Pont de Prat, BH83; Pragnères, BH54; Prat/Lahitte, BH87; Sarrancolin, BH86; Saint-Lézer, BJ60; Saint-Pé-de-Bigorre, YN37; Tournay, BH78; Vialette, La, BH66. **Huesca** : Ansó : 3 km N, XN73; Bielsa : embalse de Pineta, BH72; Bujaruelo, YN32; Candanchú, YN03; Castarnes : cruce, CH10; Formigal, YN13; Obarra, CG09; Panticosa, YN23; Piedrafita de Jaca, YN13; Pineta : parador, BH62; Plan de Escún, Garganta, BH71; Plan : puente de la Fonde, BH82; Pueyo de Jaca, YN23; Sallent de Gállego, YN13; San Juan de la Peña, y monasterio viejo, XN90; Selva de Oza : Boca del Infierno, XN84; Sigués : puente río Ezca, XN62; Siresa, XN83; Urdués : 1 km, XN83; Villanúa, YN02. **La Rioja** : Ezcaray, VM98; Leiva, VN90; Monte Toloño, junto Labastida, WN11; Posadas, VM97; San Millán de la Cogolla, WM18; Villanueva de Cameros, WN26. **Navarra** : Allí : alred. cueva Akelar, WN96; Aralar : Altxueta y Casa Forestal, WN85; Arteta, WN94; Atondo, WN94; Baraibar, WN86; Ciordia, WN64; Elizondo, XN27; Endarlaza, XN09; Etxalar, XN18; Foz de Arbayún, XN42; Foz de Minchate, XN65; Huarte Araquil, WN84; Irati, XN56; Iribas : río Ercilla, WN86; Iribas : nacedero río Ercilla, WN85; Irurzun : Monte Erga, WN95; Isaba, XN64; Ispegui, WN28; Madoz, WN95; Monreal, XN22; Nuestra Señora del Camino, XN63; Ochagavía, XN55; Olazagutia, WN64; Orbaiceta, XN45; Puerto de Otsondo, XN28; Rincón de Belagua, XN75; Roncesvalles, XN36; Santesteban, XN07; Unzué, XN12; Urbasa : km 28, WN64; Urdax, XN29; Urzainki : 1 km N, XN64; Usateguieta, WN97; Ustarroz, XN65; Usún, XN42; Valle del Roncal : entrada, XN62; Vera de Bidasoa, XN09; Yanci, XN08. **Pyrénées-Atlantiques** : Arette, XN87; Arthez-de-Béarn, XP91; Arthez-d'Asson, YN27; Arudy, YN07; Atarratze, XN77; Atherey, XN77; Aydius, YN06; Barkoxe, XN88; Bedous, XN96; Bidarrai, XN39; Bioux-Artigues, YN04; Bosque de Sansanet, XN94; Cambó, XP20; Camou-Cihigue, XN77; Castet, YN17; Col d'Osquich, XN68; Corne/Ger, YN39; Corolotz, XP40; Chibaucoa, XP10; Donibane Garazi, XN48; Eaux-Bonnes, YN16; Eaux-Chaudes, YN05; Escot, XN97; Gabas, YN05; Gelos, YN19; Gorges de Kakouetta, XN76; Gourette, YN15; Holkarte : Gorges de H.-Oladubi, XN66; Irisarry, XN49; Issor, XN97; Isturitz-Oxocelaya, XP40; Ithurraldia, XN48; Itsasu, XN29; Larrau : puerto, XN66; Leorlas/Urdax, XN29; Lescun, XN95; Lons, YP10; Louhossoa, XN39; Mauleon, XN78; Muskildi, XN68; Peyrehorade, XP52; Pic de Gillers, XN86; Portalet : fuerte, YN14; Puerto de Escale : N, XN94; Saint-Jean-le-Vieux, XN48; Sare, XN19; Sainte-Engrâce, XN86; Sainte-Engrâce : presa, XN76; Saint-Martin, XP60; Suhare, XN67; Urdos : central eléctrica, XN95; Urgazieta, XP31; Ustaritz, XP20; Zelai, XP30. **Vizcaya** : Acorda, WP20; Aldeacueva, VN68; Anboto : Campa de Larrano y alred. Galtzaikoba, WN37; Arcentales : La Toba, VN89; Areta/Bengoechea, WN07; Arminza, WP00; Aspilza, WN49; Atxarte, WN37; Axpe-Busturia, WP20; Basinagre : alred. cueva La Mora, VN79; Bérriz, WN38; Bilbao : Altamira, Arabella y Txurdinaga, WN09; Cadena, La : Pico del Moro, Ventalaperra y alred. cueva Teleférico, VN68; Calera del Prado, La, VN67; Canala, WP20; Ceánuri, WN27; Ceberio : Ermitabarri, WN17; Ciérvana, VN99; Dima : entrada cueva Barronbarro II, WN27; Ereño, WP30; Galdames : alred. cueva 6.G.74, alred. cueva Los Cuervos y montes, VN99; Gardata, WP30; Gorbea : Aldamiñape, Arraba, Itxina, Lekanda, Ojo Atxular, Paraíso de Arraba, Paso de Aldape, Paso de Mandabide, Río Padrobaso, Río Zubizola y Yondegorta, WN16; Iruzubieta, WN38; Jaureguia/Ibarra, WN07; Lamíndano, WN27; Lauquiniz, WN09; Lejona : Universidad, WN09;

Lendoño de Arriba, VN96; Lequeitio, WP40; Marquina, WN49; Nachítua, WP30; Orduña : subida a la Virgen, VN96; Pagasarri : 2 km del refugio y San Roque, WN08; Portuondo, WP20; Regato, El, y pantano superior, VN99; San Pedro de Atxerre, WP20; San Pedro de Galdames, VN98; Santa Agueda, VN98; Tellitu, VN98; Traslaviña : apeadero, VN88; Treto, VN68; Trucíos : Barranco de Laguanaz, VN89; Ubidea, WN26; Untzillaitz, WN27; Urkizu, y alred. cueva Otxas y alred. cueva Usumaltxe, WN18; Yurre, WN17; Zabalandi : hayedo, WN37; Zaramillo : alred. mina. VN98; Zolarte, WN39.

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Antarctic and Subantarctic echinoids from 'Marion Dufresne' expeditions MD03, MD04, MD08 and from the 'Polarstern' expedition Epos III

by Chantal De Ridder, Bruno David and Alberto Larrain

Abstract. — The Subantarctic and Antarctic MD03, MD04, MD08 and Epos III expeditions collected regular and irregular echinoids from the continental shelf around Marion and Prince Edward islands (MD08), Crozet islands (MD03, MD08), Kerguelen islands (MD03, MD04), and the Weddell Sea (Epos III). The collection comprises 31 species belonging to 6 families. Affinities and taxonomic position of 18 species or subspecies are discussed : *Aporocidaris antarctica, Ctenocidaris nutrix nutrix, C. nutrix longispina, C. perrieri, C. speciosa, C. spinosa, Homalocidaris gigantea, Notocidaris mortenseni, N. gaussensis, Kamptosoma asterias, Sterechinus diadema, Plexechinus planus, P.* aff. *cinctus, Pourtalesia* aff. *hispida, Amphipneustes rostratus, Brachysternaster chesheri, Parapneustes abatoides* and *Delopatagus brucei.* Geographical and bathymetrical distributions for all species are investigated and tabulated.

Résumé. — Les échinides réguliers et irréguliers récoltés lors des expéditions subantarctiques et antarctiques MD03, MD04, MD08 et Epos III sont déterminés. Les récoltes ont été effectuées sur le plateau continental autour des îles Marion et Prince Edward (MD08), Crozet (MD03, MD08), Kerguelen (MD03, MD04), et dans la mer de Weddell (Epos III). La collection comprend 31 espèces appartenant à 6 familles. Les affinités et la position taxonomique de 18 espèces ou sous-espèces sont discutées : *Aporocidaris antarctica, Ctenocidaris nutrix nutrix, C. nutrix longispina, C. perrieri, C. speciosa, C, spinosa, Homalocidaris gigantea, Notocidaris mortenseni, N. gaussensis, Kamptosoma asterias, Sterechinus diadema, Plexechinus planus, P.* aff. *cinctus, Pourtalesia* aff. *hispida, Amphipneustes rostratus, Brachysternaster chesheri, Parapneustes abatoides* and *Delopatagus brucei.* Les distributions géographique et bathymétrique de toutes les espèces sont détaillées.

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Introduction

Bionomical investigations have been made in the Antarctic and Subantarctic regions by several recent expeditions (fig. 1). The MS "Marion-Dufresne" expeditions MD03, MD04, MD08, organized by the "Terres Australes et Antarctiques Françaises" (TAAF), investigated the continental shelf and slope of some Subantarctic islands, namely Kerguelen (MD03 and MD04 in 1974 and 1975, respectively), Crozet (MD03 and MD08 in 1974 and 1979, respectively), Marion and Prince Edward (MD08 in 1979). Two additional sets of data were obtained for Kerguelen (Golfe du Morbihan et Golfe des Baleiniers) by the "Japonaise"

collections Ker72 and Ker74. The MS "Polarstern" expedition Epos III studied the Weddell Sea. This last expedition was sponsored by the European Science Foundation and by the "Alfred Wegener Institüt" (AWI) for polar and marine research; the material was sorted by the "Centre National de Tri et d'Océanographie Biologique" (CENTOB, IFREMER). One of the aims of these expeditions was a quantitative and qualitative inventory of the benthos. Details of the program, stations, sampling methods and environmental (physical and chemical) conditions are given by HUREAU (1976) for MD03, by GUILLE (1977*a*) for MD04, Ker72 and Ker74, by ARNAUD and HUREAU (1979) for MD08, by ARNTZ *et al.* (1990) for Epos III. The study area is mapped in figure 1. The echinoid collections are deposited at the Muséum national d'Histoire naturelle in Paris.

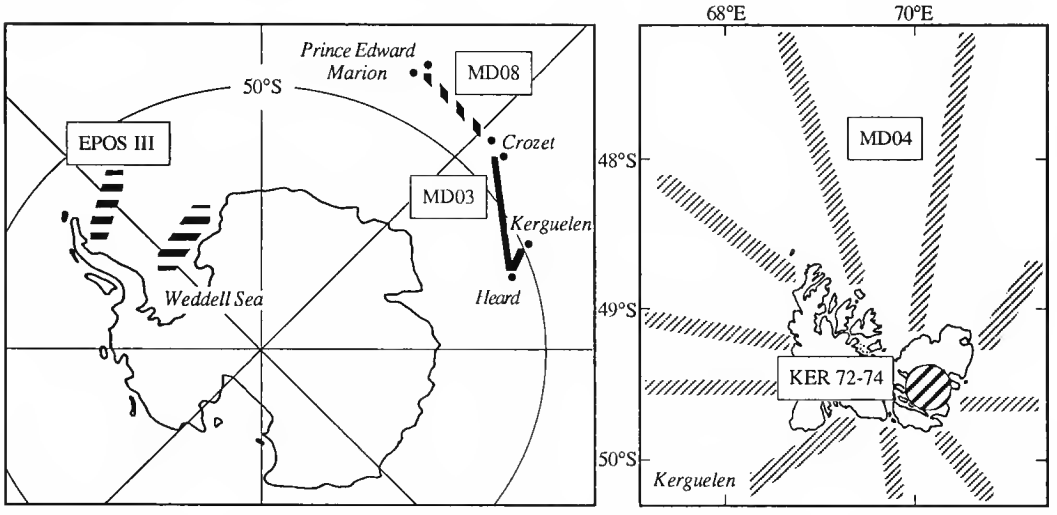

FIG. 1. — Areas prospected during the expeditions MD03, MD04, MD08, Ker72-74, and Epos III.

RESULTS

31 species of echinoids were collected in the Antarctic and Subantarctic regions during the MD03, MD04, MD08, "Japonaise" Ker72 and Ker74, and Epos III expeditions. They belong to 6 families : Cidaridae, Echinothuriidae, Echinidae, Urechinidae, Pourtalesiidae and Schizasteridae. The species and their collecting stations are listed for each expedition (see tables 1-5); their geographical (table 6) and bathymetric (fig. 5) distributions are also summarized. Species presenting taxonomic difficulties, or those rarely collected and in need of further description and illustration are discussed individually below. For the other species listed, please refer to MORTENSEN (1928*b*, 1935, 1943, 1950*b*, 1951) for more information. *Brachysternaster chesheri, Plexechinus planus* and *Urechinus mortenseni* were described subsequent to MORTENSEN's monograph, see LARRAIN (1985), MIRONOV (1978) and DAVID & MOOI (1990), respectively.

TABLE 1. — Inventories of the collected species and lists of stations of expedition MD03 at Kerguelen and Crozet islands (asterisks indicate that a part of the sample corresponds to broken specimens or fragments).

Station	Long.	Lat.	Depth	Number of specimens
		CIDARIDAE		
		Aporocidaris antarctica		
St. 13	65°39′9 E	50°49′1 S	3240 m	3
		Ctenocidaris nutrix nutrix		
St. 2	70°44′7 E	49°30′7 S	115 m	5
St. 2	70°47′1 E	49°33′2 S	130 m	5
St. 3	71°51′7 E	49°25′4 S	650-620 m	1
St. 7	75°38′4 E	52°12′7 S	560-525 m	38
St. 14	64°57′9 E	49°48′4 S	250 m	3
St. 14	64°50′6 E	49°45′8 S	262 m	1
St. 17	66°04′0 E	47°24′9 S	585 m	3
St. 22	70°51′1 E	48°58′5 S	105-90 m	34
St. 23	70°01′9 E	49°59′2 S	158 m	8
St. 24	69°48′7 E	50°10′7 S	195 m	56
		ECHINOTHURIIDAE		
		Kamptosoma asterias		
St. 12	69°35′7 E	55°49′5 S	4200-4225 m	8
		ECHINIDAE		
		Sterechinus neumayeri		
St. 2	70°47′1 E	49°33′2 S	130 m	67
St. 8	73°42′0 E	52°58′0 S	123 m	2
St. 14	64°57′9 E	49°48′4 S	250 m	4
St. 14	64°50′6 E	49°45′8 S	262 m	3
St. 18	68°07′1 E	47°42′2 S	243 m	5
St. 21	70°55′4 E	48°29′7 S	360-345 m	21*
St. 22	70°51′1 E	48°58′5 S	105-90 m	94*
St. 23	70°01′9 E	49°59′2 S	158 m	71
St. 24	69°48′7 E	50°10′7 S	195 m	19*
St. 26	51°59′0 E	46°24′0 S	180 m	10
St. 26	51°58′3 E	46°23′3 S	165 m	1
St. 28	51°29′0 E	46°18′1 S	400 m	5
St. 30	50°50′2 E	46°02′3 S	187 m	13
St. 31	50°32′8 E	45°57′2 S	110 m	5*
		URECHINIDAE		
		Plexechinus aff. **cinctus**		
St. 17	66°04′0 E	47°24′9 S	585 m	1*

		POURTALESIIDAE		
		Pourtalesia cf. hispida		
St. 12	69°35′7 E	55°49′5 S	4200-4225 m	1*
St. 13	65°39′9 E	50°49′1 S	3240 m	6*
		SCHIZASTERIDAE		
		Abatus cordatus		
St. 7	75°38′4 E	52°12′7 S	560-525 m	4
St. 8	73°42′0 E	52°58′0 S	123 m	8
St. 8	73°38′0 E	52°59′4 S	90 m	5
St. 10	72°50′1 E	53°06′7 S	255 m	1*
St. 17	66°04′0 E	47°24′9 S	585 m	1*
		Brisaster kerguelensis		
St. 3	71°51′7 E	49°25′4 S	650-620 m	16*
St. 6	71°35′8 E	50°37′9 S	565 m	1*
St. 7	75°38′4 E	52°12′7 S	560-525 m	1*
St. 17	66°04′0 E	47°24′9 S	585 m	1*
St. 18	68°07′1 E	47°42′2 S	243 m	1

TABLE 2. — Inventories of the collected species and lists of stations of expedition MD04 at Kerguelen islands (the precise depths of stations 105 to 107 are unknown).

Station	Long.	Lat.	Depth	Number of specimens
		CIDARIDAE		
		Ctenocidaris nutrix nutrix		
St. 2	70°22′2 E	49°29′3 S	44 m	7*
St. 3	70°33′2 E	49°28′8 S	75 m	7
St. 4	70°40′5 E	49°29′8 S	96 m	4
St. 5	70°56′0 E	49°30′0 S	147 m	4*
St. 5	70°54′5 E	49°30′6 S	140 m	2
St. 7	70°57′0 E	49°32′1 S	149-155 m	19
St. 14	69°44′6 E	49°44′4 S	103 m	2
St. 15	69°47′2 E	49°54′8 S	120 m	3
St. 16	69°49′2 E	50°02′7 S	166 m	3
St. 21	69°18′3 E	49°41′4 S	110 m	1*
St. 23	68°48′5 E	49°55′5 S	155 m	1
St. 24	68°29′0 E	50°04′0 S	195 m	9*
St. 25	68°17′2 E	50°08′8 S	255 m	6
St. 26	68°28′3 E	50°03′4 S	192-198 m	3*
St. 26	68°25′0 E	50°05′8 S	207 m	50*
St. 34	68°10′7 E	49°27′4 S	185 m	1
St. 35	67°53′1 E	49°28′0 S	191 m	1
St. 37	67°19′9 E	49°26′5 S	301 m	1
St. 44	68°03′5 E	49°04′0 S	175-192 m	6
St. 45	67°30′4 E	49°00′3 S	206 m	2

St. 47	67°07′9 E	48°59′1 S	315 m	8*
St. 51	68°45′1 E	48°44′0 S	95 m	2
St. 52	68°31′2 E	48°37′2 S	125 m	4
St. 57	67°32′5 E	48°07′0 S	365 m	1
St. 65	69°04′0 E	48°01′0 S	177 m	1
St. 101	70°45′6 E	49°03′4 S	84 m	1
St. 102	70°50′8 E	48°56′6 S	95 m	2
St. 108	70°41′3 E	49°03′4 S	76 m	1
St. 113	70°19′8 E	49°51′0 S	145 m	rad.
St. 114	70°24′4 E	49°54′5 S	168 m	5*
St. 116	70°34′6 E	50°02′0 S	346 m	1
St. 118	70°28′7 E	49°58′6 S	245-185 m	22
St. 119	70°19′0 E	49°49′9 S	131 m	1

ECHINIDAE

Sterechinus neumayeri

St. 3	70°33′2 E	49°28′8 S	75 m	2
St. 5	70°54′5 E	49°30′6 S	140 m	4
St. 8	69°38′3 E	49°31′2 S	21 m	2
St. 8	69°38′3 E	49°31′2 S	22 m	3
St. 9	69°39′4 E	49°32′2 S	110 m	2
St. 10	69°40′8 E	49°33′2 S	49 m	7
St. 14	69°44′6 E	49°44′4 S	103 m	7
St. 15	69°47′2 E	49°54′8 S	120 m	6
St. 23	68°48′5 E	49°55′5 S	155 m	2
St. 24	68°29′0 E	50°04′0 S	195 m	3*
St. 26	68°25′0 E	50°05′8 S	207 m	37*
St. 27	69°14′0 E	49°32′9 S	176-170 m	10
St. 47	67°07′9 E	48°59′1 S	315 m	2
St. 48	67°17′6 E	49°00′4 S	239 m	2*
St. 52	68°31′2 E	48°37′2 S	125 m	4
St. 59	68°38′6 E	48°41′4 S	104 m	3
St. 62	69°11′6 E	48°40′1 S	75 m	2
St. 62	69°11′3 E	48°40′6 S	61 m	1
St. 70	68°56′5 E	47°42′2 S	204 m	3
St. 72	69°12′0 E	48°46′6 S	57 m	5
St. 74	69°01′1 E	49°02′3 S	30 m	3
St. 75	69°08′0 E	48°58′1 S	211 m	1
St. 76	69°08′0 E	48°54′6 S	125-89 m	10
St. 77	69°10′5 E	48°51′3 S	190 m	3
St. 78	69°12′3 E	48°45′7 S	46-54 m	3
St. 79	69°21′3 E	49°04′0 S	37 m	6
St. 84	69°56′5 E	49°08′3 S	50 m	1
St. 88	69°59′3 E	48°54′6 S	87 m	5
St. 90	70°09′0 E	48°20′9 S	128 m	1*
St. 91	70°14′0 E	48°02′0 S	151 m	1
St. 93	70°15′7 E	47°44′8 S	164-162 m	10
St. 108	70°41′3 E	49°03′4 S	76 m	31
St. 113	70°21′2 E	49°50′2 S	147 m	3
St. 113	70°19′8 E	49°51′0 S	145 m	frag.
St. 114	70°24′4 E	49°54′5 S	168 m	2
St. 118	70°28′7 E	49°58′6 S	245-185 m	14
St. 119	70°19′0 E	49°49′9 S	131 m	4

POURTALESIIDAE

Pourtalesia sp.

St. 26	68°25′0 E	50°05′8 S	207 m	2
St. 57	67°32′5 E	48°07′0 S	365 m	frag.

SCHIZASTERIDAE

Abatus cordatus

St. 5	70°54′5 E	49°30′6 S	140 m	1
St. 8	69°38′3 E	49°31′2 S	21 m	4*
St. 8	69°38′3 E	49°31′2 S	22 m	4
St. 9	69°39′4 E	49°32′2 S	110 m	1
St. 10	69°40′8 E	49°33′2 S	58 m	1
St. 10	69°40′8 E	49°33′2 S	49 m	1
St. 12	69°40′3 E	49°39′8 S	36 m	4
St. 13	69°43′3 E	49°41′3 S	72 m	2
St. 18	69°20′4 E	49°35′4 S	21 m	22*
St. 18	69°20′5 E	49°35′2 S	18 m	4*
St. 18	69°20′5 E	49°35′2 S	19 m	1
St. 19	69°20′5 E	49°36′0 S	67 m	14*
St. 19	69°20′7 E	49°36′1 S	70 m	1*
St. 23	68°48′5 E	49°55′5 S	155 m	1
St. 30	68°50′1 E	49°27′7 S	35 m	1
St. 31	68°46′8 E	49°27′4 S	63 m	15*
St. 31	68°46′5 E	49°27′3 S	68 m	1
St. 42	68°47′5 E	49°09′3 S	140 m	1
St. 49	68°52′2 E	48°48′4 S	60 m	3
St. 49	68°52′2 E	48°48′2 S	65 m	2*
St. 52	68°31′2 E	48°37′2 S	125 m	1
St. 54	67°53′1 E	48°19′7 S	185 m	1
St. 60	69°02′2 E	48°41′0 S	18 m	5*
St. 60	69°02′2 E	48°41′0 S	17 m	10*
St. 61	69°03′5 E	48°40′5 S	51 m	2
St. 61	69°03′5 E	48°40′4 S	48 m	1
St. 73	69°04′0 E	49°06′3 S	35 m	15
St. 73	69°04′0 E	49°06′3 S	30 m	11
St. 74	69°01′1 E	49°02′3 S	31 m	3
St. 74	69°01′1 E	49°02′3 S	30 m	1
St. 76	69°08′0 E	48°54′6 S	125-89 m	1
St. 79	69°21′3 E	49°04′0 S	43 m	2*
St. 79	69°21′3 E	49°04′0 S	37 m	1
St. 82	69°31′1 E	48°55′4 S	209-305 m	3
St. 83	69°55′6 E	49°10′9 S	24 m	73*
St. 86	69°58′0 E	49°02′9 S	95 m	4*
St. 90	70°09′0 E	48°20′9 S	128 m	1
St. 100	70°40′5 E	49°03′6 S	74 m	1
St. 110	70°34′0 E	49°10′0 S	18 m	17*
St. 110	70°34′0 E	49°10′0 S	22 m	38*
St. 113	70°19′8 E	49°51′0 S	145 m	frag.
St. 121	70°08′1 E	49°41′8 S	16-17 m	17

Brisaster kerguelensis

St. 26	68°25′0 E	50°05′8 S	207 m	9
St. 66	68°58′5 E	47°41′5 S	200 m	5
St. 70	68°56′5 E	47°42′2 S	204 m	1
St. 76	69°08′0 E	48°54′6 S	125-89 m	1
St. 89	70°04′7 E	48°38′1 S	105 m	1
St. 89	70°06′0 E	48°38′0 S	105 m	2
St. 90	70°09′0 E	48°19′3 S	128 m	1
St. 92	70°15′7 E	47°44′8 S	164 m	2
St. 92	70°15′8 E	47°44′9 S	164 m	1*
St. 93	70°15′7 E	47°44′8 S	164-162 m	2
St. 94	70°23′8 E	47°26′5 S	170 m	33*
St. 95	70°27′5 E	47°09′7 S	188 m	2*
St. 98	70°30′2 E	46°47′7 S	1218 m	4
St. 105	71°06′5 E	48°43′9 S	.....?	frag.
St. 106	71°06′5 E	48°43′5 S	.....?	13
St. 107	71°18′5 E	48°32′3 S	.....?	frag.
St. 115	70°29′1 E	49°58′0 S	234 m	2

TABLE 3. — Inventories of the collected species and lists of stations of expedition MD08 at Marion, Prince Edward and Crozet islands.

Station	Long.	Lat.	Depth	Number of specimens
		ECHINIDAE		
		Sterechinus neumayeri		
St. 9	51°50′5 E	46°22′8 S	75-104 m	1
St. 9	51°49′6 E	46°10′8 S	120-150 m	6
St. 9	51°54′3 E	46°22′4 S	150-160 m	7
St. 9	51°52′3 E	46°19′8 S	150-340 m	13
St. 11	37°53′9 E	46°52′2 S	115-120 m	2
St. 12	37°54′1 E	46°55′7 S	103 m	73
St. 13	37°55′6 E	46°56′3 S	120 m	88
St. 15	38°00′0 E	46°57′7 S	185-210 m	52
St. 15	37°59′9 E	46°57′7 S	204 m	9
St. 16	37°59′1 E	46°50′2 S	138-142 m	18
St. 17	37°53′8 E	46°52′1 S	112 m	4
St. 17	37°53′5 E	46°52′5 S	110 m	3
St. 18	37°56′2 E	46°49′8 S	140 m	34
St. 18	37°56′4 E	46°49′8 S	138 m	4
St. 19	38°03′7 E	46°45′9 S	190 m	9
St. 20	38°03′5 E	46°47′2 S	180 m	17
St. 21	37°52′9 E	46°52′9 S	50 m	2
St. 21	37°52′8 E	46°53′3 S	50 m	5
St. 22	37°51′9 E	46°52′4 S	31 m	5
St. 23	38°01′3 E	46°57′9 S	250-460 m	1
St. 25	37°56′6 E	46°45′3 S	185-232 m	121
St. 26	38°00′6 E	46°50′6 S	135-145 m	41
St. 28	37°57′2 E	46°43′5 S	246-285 m	3

St. 31	37°46′6 E	46°59′5 S	185 m	2
St. 32	37°46′8 E	46°59′0 S	83-100 m	9
St. 33	37°51′5 E	46°52′2 S	45 m	1
St. 34	37°51′2 E	46°50′2 S	115 m	33
St. 34	37°51′2 E	46°50′2 S	110 m	10
St. 35	38°00′3 E	46°39′7 S	53 m	8
St. 36	38°06′7 E	46°40′7 S	570-315 m	4
St. 36	38°07′2 E	46°40′9 S	570-375 m	2
St. 42	51°34′9 E	46°21′4 S	172-220 m	45
St. 48	50°37′1 E	46°05′0 S	200-140 m	23
St. 50	50°37′8 E	45°51′5 S	150 m	1
St. 53	50°20′6 E	46°07′5 S	110 m	1
St. 66	49°13′3 E	46°15′3 S	500-562 m	1*
St. 72	50°32′0 E	46°23′4 S	187-155 m	2
St. 73	50°37′8 E	46°24′3 S	263-412 m	10
St. 74	50°47′8 E	46°17′8 S	290 m	4
St. 75	51°52′9 E	46°19′9 S	155-257 m	15
St. 75	51°52′0 E	46°21′0 S	145-135 m	2
St. 78	51°58′1 E	46°23′7 S	142-170 m	3
St. 79	51°53′8 E	46°24′6 S	100 m	3

SCHIZASTERIDAE

Brisaster kerguelensis

St. 9	51°51′2 E	46°22′9 S	125 m	1*
St. 40	51°33′9 E	46°21′1 S	190 m	1*
St. 43	51°11′0 E	46°18′5 S	1400-1500 m	13*
St. 44	51°14′0 E	46°18′0 S	1500 m	1*
St. 46	50°44′7 E	46°10′6 S	375-390 m	10*
St. 57	50°05′3 E	45°46′2 S	195-200 m	2*
St. 59	49°59′3 E	45°59′9 S	210-217 m	2*
St. 60	49°48′2 E	46°02′7 S	245-250 m	2
St. 67	49°37′4 E	46°16′8 S	277-280 m	1
St. 70	50°28′4 E	46°46′6 S	1350-1440 m	7*
St. 71	50°39′0 E	46°37′5 S	268-270 m	2*
St. 72	50°32′0 E	46°23′4 S	187-155 m	8*

Tripylaster philippi

St. 18	37°56′2 E	46°49′8 S	140 m	2*
St. 28	37°58′4 E	46°42′6 S	257-280 m	1*
St. 31	37°46′6 E	46°59′5 S	185 m	1*

TABLE 4. — Inventories of the collected species and lists of stations of expeditions "Japonaise" 1972 & 1974 at Kerguelen islands.

Station	Depth	Number of specimens
CIDARIDAE		
Ctenocidaris nutrix nutrix		
Golfe du Morbihan (7 stations)	23-270 m	13*
ECHINIDAE		
Sterechinus neumayeri		
Off Ratmanoff (1 station)	250-270 m	4
Golfe du Morbihan (1 station)	46 m	1
Golfe des Baleiniers (2 stations)	34-38 m	2*
SCHIZASTERIDAE		
Abatus cordatus		
Golfe du Morbihan (82 stations)	6-175 m	94*
Golfe des Baleiniers (14 stations)	1-50 m	45*

TABLE 5. — Inventories of the collected species and lists of stations of expedition Epos III in the Weddell Sea.

Station	Long.	Lat.	Depth	Number of specimens
CIDARIDAE				
Ctenocidaris nutrix longispina				
St. 229	26°16′7 W	75°15′7 S	498 m	1
St. 235	27°34′7 W	75°09′1 S	404-407 m	2
St. 241	28°00′3 W	75°02′9 S	451-453 m	6
St. 256	27°36′4 W	75°10′9 S	399-382 m	1
St. 257	27°59′1 W	75°08′2 S	460-457 m	1
St. 270	20°45′1 W	73°21′3 S	294-305 m	3
St. 275	12°34′7 W	71°39′5 S	301-330 m	1
Ctenocidaris perrieri				
St. 217	46°58′1 W	60°37′6 S	232-239 m	2
St. 224	13°04′2 W	71°15′8 S	185-187 m	7
St. 229	26°13′3 W	74°14′8 S	500-506 m	2
St. 248	29°31′3 W	74°39′9 S	593-602 m	2
St. 271	20°59′4 W	73°17′0 S	352-399 m	1
St. 273	21°03′9 W	73°34′8 S	193-197 m	3
St. 275	12°34′7 W	71°39′5 S	301-330 m	3
St. 284	13°14′0 W	71°12′0 S	402-412 m	1

Ctenocidaris cf. **rugosa**

St. 217	46°58′1 W	60°37′6 S	232-239 m	1
St. 250	29°39′9 W	74°35′1 S	799-810 m	1

Ctenocidaris speciosa

St. 217	46°58′1 W	60°37′6 S	232-239 m	1
St. 226	25°58′3 W	75°15′9 S	569-574 m	1
St. 229	26°16′7 W	75°15′7 S	498 m	1
St. 248	29°31′3 W	74°39′9 S	593-602 m	8
St. 249	29°38′2 W	74°37′4 S	701-708 m	5
St. 250	29°39′9 W	74°35′1 S	799-810 m	2
St. 261	29°35′5 W	74°36′5 S	798-810 m	15*
St. 269	19°49′4 W	72°54′7 S	602-617 m	3

Ctenocidaris spinosa

St. 274	12°09′4 W	71°38′8 S	196-212 m	1
St. 275	12°34′7 W	71°39′5 S	301-330 m	5
St. 281	12°21′1 W	71°39′0 S	389-423 m	1

Ctenocidaris sp.

St. 217	46°58′1 W	60°37′6 S	232-239 m	2
St. 258	29°36′6 W	74°40′2 S	484-509 m	1

Homalocidaris gigantea

St. 217	46°58′1 W	60°37′6 S	232-239 m	2
St. 235	27°34′7 W	75°09′1 S	404-407 m	1
St. 258	29°36′6 W	74°40′2 S	484-509 m	4
St. 271	20°59′4 W	73°17′0 S	352-399 m	3
St. 270	20°45′1 W	73°21′3 S	294-305 m	1
St. 275	12°34′7 W	71°39′5 S	301-330 m	1
St. 291	12°33′5 W	71°06′1 S	499-515 m	3

Homalocidaris cf. **gigantea**

St. 248	29°31′3 W	74°39′9 S	593-602 m	1*

Notocidaris gaussensis

St. 252	29°41′9 W	74°28′2 S	1153-1223 m	1

Notocidaris mortenseni

St. 226	25°53′5 W	75°17′1 S	593-624 m	1
St. 226	25°58′3 W	75°15′9 S	569-574 m	4
St. 248	29°31′3 W	74°39′9 S	593-602 m	8
St. 249	29°42′5 W	74°36′2 S	699-712 m	2
St. 290	12°34′0 W	71°05′9 S	522-531 m	2
St. 291	12°33′5 W	71°06′1 S	499-515 m	6

ECHINIDAE

Sterechinus agassizi

St. 312	00°06′3 W	54°43′9 S	471-320 m	3

Sterechinus antarcticus

St. 217	46°58′1 W	60°37′6 S	232-239 m	1
St. 224	13°04′2 W	71°15′8 S	185-187 m	1*

St. 226	25°58′3 W	75°15′9 S	569-574 m	18
St. 229	26°12′5 W	75°14′9 S	500-509 m	4
St. 229	26°16′7 W	75°15′7 S	498 m	7
St. 230	26°59′4 W	75°14′2 S	270-280 m	12
St. 230	26°38′9 W	75°14′5 S	275-279 m	3
St. 235	27°34′7 W	75°09′1 S	404-407 m	3
St. 241	27°59′5 W	75°07′1 S	457-462 m	6
St. 241	28°00′3 W	75°02′9 S	451-453 m	10
St. 245	29°41′6 W	74°39′7 S	483-484 m	3
St. 249	29°42′5 W	74°36′2 S	699-712 m	53
St. 249	29°38′2 W	74°37′4 S	701-708 m	23
St. 250	29°39′9 W	74°35′1 S	799-810 m	23
St. 250	29°35′6 W	74°36′3 S	794-805 m	61
St. 252	29°41′9 W	74°28′2 S	1153-1223 m	26
St. 253	29°41′4 W	74°09′5 S	1996-2012 m	33
St. 256	27°36′4 W	75°10′9 S	382-399 m	1*
St. 258	29°36′6 W	74°40′2 S	484-509 m	10
St. 259	29°16′8 W	74°40′2 S	587-611 m	1
St. 261	29°35′5 W	74°36′5 S	798-810 m	23
St. 269	19°49′4 W	72°54′7 S	602-617 m	8
St. 270	20°45′1 W	73°21′3 S	294-305 m	28
St. 272	21°33′6 W	73°26′9 S	406-409 m	3
St. 273	21°03′9 W	73°34′8 S	193-197 m	261
St. 274	12°09′4 W	71°38′8 S	196-212 m	19
St. 275	12°34′7 W	71°39′5 S	301-330 m	22
St. 281	12°21′1 W	71°39′5 S	402-450 m	19
St. 282	12°27′4 W	71°31′7 S	609-575 m	2
St. 284	13°14′0 W	71°12′0 S	402-412 m	13
St. 289	13°27′9 W	71°12′0 S	672-677 m	40
St. 290	12°34′0 W	71°05′9 S	522-531 m	17
St. 291	12°33′5 W	71°06′2 S	499-515 m	42
St. 293	12°53′8 W	71°06′2 S	771-793 m	65

Urechinidae

Plexechinus nordenskjoldi

St. 217	46°56′1 W	60°37′6 S	232-239 m	33
St. 252	29°41′9 W	74°28′2 S	1153-1223 m	29
St. 261	29°35′5 W	74°36′5 S	798-810 m	2
St. 289	13°27′9 W	71°12′0 S	672-677 m	1
St. 291	12°33′5 W	71°06′2 S	499-515 m	1

Plexechinus planus

St. 252	29°41′9 W	74°28′2 S	1153-1223 m	19
St. 295	13°48′1 W	71°08′8 S	2037-2025 m	3

Urechinus mortenseni

St. 249	29°38′2 W	74°37′4 S	701-708 m	1
St. 252	29°41′9 W	74°28′2 S	1153-1223 m	2

Urechinus wyvilli

St. 253	29°41′4 W	74°09′5 S	1996-2012 m	10
St. 295	13°48′1 W	71°08′8 S	2037-2025 m	2

POURTALESIIDAE

Pourtalesia aff. hispida

St. 252	29°41′9 W	74°28′2 S	1153-1223 m	7

SCHIZASTERIDAE

Abatus cavernosus

St. 217	46°56′1 W	60°37′6 S	232-239 m	1

Amphipneustes bifidus

St. 258	29°36′6 W	74°40′2 S	484-509 m	1
St. 272	21°33′6 W	73°26′9 S	406-409 m	2
St. 275	12°34′7 W	71°39′5 S	301-330 m	1
St. 281	12°21′1 W	71°39′5 S	402-450 m	1
St. 284	13°14′0 W	71°12′0 S	402-412 m	1
St. 290	12°34′0 W	71°05′9 S	522-531 m	1

Amphipneustes lorioli

St. 211	55°20′1 W	60°59′8 S	182-213 m	1
St. 217	46°56′1 W	60°37′6 S	232-239 m	12*
St. 235	27°33′2 W	75°08′9 S	399-404 m	1
St. 235	27°34′7 W	75°09′1 S	404-407 m	8
St. 241	28°00′3 W	75°02′9 S	451-453 m	4
St. 250	29°39′9 W	74°35′1 S	799-810 m	3
St. 253	29°41′4 W	74°09′5 S	1996-2012 m	1
St. 256	27°36′4 W	75°10′9 S	382-399 m	4*
St. 261	29°35′5 W	74°36′5 S	798-810 m	10
St. 273	21°03′9 W	73°34′8 S	193-197 m	1

Amphipneustes rostratus

St. 235	27°34′7 W	75°09′1 S	404-407 m	1
St. 248	29°31′3 W	74°39′9 S	593-602 m	3
St. 249	29°42′5 W	74°36′2 S	699-712 m	1
St. 249	29°38′2 W	74°37′4 S	701-708 m	2
St. 250	29°39′9 W	74°35′1 S	799-810 m	12
St. 252	29°41′9 W	74°28′2 S	1153-1223 m	11
St. 261	29°35′5 W	74°36′5 S	798-810 m	35
St. 272	21°33′6 W	73°26′9 S	406-409 m	2
St. 290	12°34′0 W	71°05′9 S	522-531 m	1

Amphipneustes similis

St. 211	55°20′1 W	60°59′8 S	182-213 m	3
St. 217	46°56′1 W	60°37′6 S	232-239 m	1
St. 235	27°34′7 W	75°09′1 S	404-407 m	5
St. 241	27°59′5 W	75°07′1 S	457-462 m	1

Brachysternaster chesheri

St. 217	46°56′1 W	60°37′6 S	232-239 m	2*
St. 235	27°34′7 W	75°09′1 S	404-407 m	4
St. 241	28°00′3 W	75°02′9 S	451-453 m	2
St. 250	29°35′6 W	74°36′3 S	794-805 m	1
St. 252	29°41′9 W	74°28′2 S	1153-1223 m	19
St. 256	27°36′4 W	75°10′9 S	382-399 m	1
St. 261	29°35′5 W	74°36′5 S	798-810 m	37

		Delopatagus brucei		
St. 253	29°41′4 W	74°09′5 S	1996-2012 m	2
		Parapneustes abatoides		
St. 211	55°20′1 W	60°59′8 S	182-213 m	1
St. 217	46°56′1 W	60°37′6 S	232-239 m	2
St. 248	29°31′3 W	74°39′9 S	593-602 m	3
St. 249	29°38′2 W	74°37′4 S	701-708 m	1
St. 250	29°39′9 W	74°35′1 S	799-810 m	16
St. 250	29°35′6 W	74°36′3 S	794-805 m	1
St. 261	29°35′5 W	74°36′5 S	798-810 m	8

Taxonomic comments

The affinities and taxonomic position of 18 species or subspecies : *Aporocidaris antarctica, Ctenocidaris nutrix nutrix, C. nutrix longispina, C. perrieri, C. speciosa, C. spinosa, Homalocidaris gigantea, Notocidaris mortenseni, N. gaussensis, Kamptosoma asterias, Sterechinus diadema, Plexechinus planus, P.* aff. *cinctus, Pourtalesia* aff. *hispida, Amphipneustes rostratus, Brachysternaster chesheri, Parapneustes abatoides* and *Delopatagus brucei* are discussed.

Aporocidaris antarctica Mortensen, 1909

Aporocidaris antarctica Mortensen, 1909 : 25, pl. 3 figs 5-7, pl. 5 figs 2, 9-11, pl. 7 figs 4-5, pl. 10 figs 6, 9, pl. 11 figs 10, pl. 13 figs 3, 6, pl. 14 figs 1, 16, 17, pl. 15 figs 8, 12-13, 16, 24-28, pl. 16 fig. 15; Mortensen, 1928*b* : 116.

This species was known only from the 12 specimens collected by the 'Deutsche Südpolar Expedition' at 2725-3486 m depth (Mortensen, 1909) and supposedly by some other material from previous collections (Mortensen, 1928*b*). The specimens from the MD03 expedition extend the known geographical distribution of this species, for they were collected in the same quadrant of the Antarctic Sea, but far to the north, close to the Antarctic convergence. Work in progress (A.L.) on this species shows that its systematic status is precarious.

CTENOCIDARIS Mortensen, 1910

This genus comprises 7 species which appear closely related to each other. They differ mainly in the shape and ornamentation of the oral primary spines, in the length and ornamentation of the coronal primary spines, and, in some species, in the arrangement of the apical plates (Mortensen, 1928*b*). Differences and similarities between *C. nutrix nutrix* and *C. nutrix longispina*, as well as between *C. perrieri, C. speciosa* and *C. spinosa* are discussed below.

Ctenocidaris nutrix nutrix (Wyville Thomson, 1876)

Cidaris nutrix Wyville Thomson, 1876 : 62.
Stereocidaris nutrix; MORTENSEN, 1903 : 25, 29, 173, pl. 10 figs 3-4, 12, 14, 24.
Eurocidaris nutrix; MORTENSEN, 1909 : 30, pl. 3 fig. 9, pl. 4 figs 5-6, pl. 6 figs 2, 4-9, 11-12, pl. 10 figs 7, 11, pl. 11 fig. 12, pl. 13 fig. 7, pl. 15 figs 17, 20-23.
Ctenocidaris (*Eurocidaris*) *nutrix*; MORTENSEN, 1928*b* : 128.

Ctenocidaris nutrix longispina (Mortensen, 1928*a*)
(Pl. I, 1-3)

Eurocidaris nutrix var. *longispina* Mortensen, 1928*a* : 67.
Ctenocidaris (*Eurocidaris*) *nutrix* var. *longispina*; MORTENSEN, 1928*b* : 129, pl. 57 fig. 8.

The original diagnostic character (length of the primary coronal spines) for these two subspecies is unreliable. Later, MORTENSEN (1928*b*) found differences in the position of the ocular plates (all insert in *C. nutrix longispina*, while they are usually exsert in *C. nutrix nutrix*). Our identification of the specimens from Epos III is based on this latter characteristic (pl. I, 2). However, the distinction between the two subspecies is weakly grounded (as already noticed by CLARK, 1925), and it may be necessary to reconsider their status.

Ctenocidaris perrieri Kœhler, 1912*a*
(Pl. II, 1-3)

Ctenocidaris perrieri Kœhler, 1912*a* : 161; KŒHLER, 1912*b* : 150, pl. 12 figs 4-8, pl. 13 figs 2-8, pl. 14 figs 9-14, pl. 15 figs 1-10; MORTENSEN, 1928*b* : 123, pl. 69 fig. 23

Ctenocidaris speciosa Mortensen, 1910
(Pl. III, 1-3)

Ctenocidaris speciosa Mortensen, 1910 : 4, pls 1-2, pl. 3 figs 1-3, pl. 8; MORTENSEN, 1928*b* : 122.

Ctenocidaris spinosa (Kœhler, 1926)
(Pl. IV, 1-2)

Notocidaris spinosa Kœhler, 1926 : 14, pl. 97 figs 1-6, pl. 98 figs 1-7, pl. 99 figs 1-3, pl. 112 fig. 7, pl. 114 fig. 7, pl. 119 fig. 6.
Ctenocidaris spinosa; MORTENSEN, 1928*b* : 124, pl. 12 fig. 13, pl. 77 figs 10-12.

C. spinosa was previously known only from the 'Aurora' specimens. MORTENSEN (1928*b*) stated that *C. perrieri* is probably the nearest related to *C. speciosa* and that both are very close to *C. spinosa*. We distinguish these three species on the basis of size and spinulation of the coronal primary spines, the shape and ornamentation of the oral primary spines, the

tuberculation close to the median interradial suture, and the color of the test. *C. spinosa* possesses densely and strongly thorny primary coronal spines (pl. IV, 1); denticules are sharp, arranged in ca. 8 longitudinal series that may fuse into ridges. Oral primaries are spear-shaped and bear sharp, lined spinules, these spinules sometimes fused into two lateral wings (pl. IV, 2). A supplementary character, not mentioned by MORTENSEN (1928*b*), is noted : there is a conspicuous naked area on both sides of the interradial suture. The color is typically brownish purple. *C. perrieri* differs from *C. spinosa* in having slender coronal primaries which show a less regular arrangement of their spinules (lack of ridges), blunter spinules on the oral primaries (pl. II, 3), tuberculation which reaches the interradial suture (lack of naked areas), and a yellowish color. *C. speciosa* has finely serrated coronal primaries (pl. III, 1-2), flattened oral primaries bearing blunt, coarse spinules (pl. III, 3). The median interradial area and the color of the specimens are similar to those of *C. perrieri.*

Homalocidaris gigantea (Clark, 1925)
(Pl. IV, 3-4)

Austrocidaris gigantea Clark, 1925 : 28, pl. 3 figs 1-2.
Homalocidaris gigantea; MORTENSEN, 1928*b* : 137, pl. 11 fig. 6, pl. 77 fig. 14, pl. 83 fig. 23; MORTENSEN, 1950*a* : 297, pl. 7 figs 4-6.

This species was only known by two specimens sampled by the 'Discovery' near Victoria Land in the Ross Sea at 180 m depth (CLARK, 1925) and by two specimens sampled by the BANZAR expedition in the Bellingshausen Sea off Palmer Archipelago (MORTENSEN, 1950*a*). The third record corresponds to the 15 specimens collected during the Epos III expedition in the Weddell Sea. These specimens fit closely the description given by CLARK (1925) and completed by MORTENSEN (1928*b*). Their simultaneous occurrence in two distinct quadrants indicate that the distribution of the species is probably circum-Antarctic.

NOTOCIDARIS Mortensen, 1909

Notocidaris mortenseni (Kœhler, 1900)

Goniocidaris mortenseni Kœhler, 1900 : 816; KŒHLER, 1901 : 5, pl. 1 fig. 1 pl. 2, fig. 11, pl. 3 fig. 17, pl. 4 fig. 29, pl. 5 fig. 30.
Stereocidaris mortenseni; MORTENSEN, 1903 : 27, 29, pl. 8 fig. 34.
Notocidaris mortensi; MORTENSEN, 1909 : 21, pl. 3 figs 1, 8, 10, pl. 14 figs 3, 6; MORTENSEN, 1928*b* : 131, pl. 11 figs 13-15, pl. 68 fig. 15.

Notocidaris gaussensis Mortensen, 1909
(Pl. V, 1-2)

Notocidaris gaussensis Mortensen, 1909 : 18, pl. 1, pl. 2 figs 1-2, pl. 5 figs 13-16, 19-21, pl. 7 fig. 2, pl. 10 figs 5, 8, pl. 11 fig. 3, pl. 13 fig. 1, pl. 14 figs 2, 4, 10, 15, pl. 15 fig. 10, pl. 18 figs 9-11, 14, 17-18; MORTENSEN, 1928*b* : 134.

The features of the upper primary spines given by MORTENSEN (1928*b*) to separate *N. mortenseni* from *N. gaussensis* are confusing because the ornamentation of these spines varies. These species differ markedly in their upper and oral primaries. *N. gaussensis* has wingless upper primaries that are usually smooth all along the shaft and sometimes distally flattened (pl. V, 1). Oral primaries are spear-shaped, slightly curved, and smooth (pl. V, 2). *N. mortenseni* has upper primaries bearing large, coarse spinules that may fuse together into wing-like extensions. Oral primaries are keeled (two opposite keels), triangularly spear-shaped, straight, and serrated at their basis. Some variations exist; one *N. mortenseni* (among the 8 specimens of station 248) has simple upper primaries and gently curved oral primaries, widened centrally, and more or less diamond shaped.

Kamptosoma asterias (A. Agassiz, 1881)

Phormosoma asterias A. Agassiz, 1881 : 104, pl. 12a figs 7-9.
Kamptosoma asterias; MORTENSEN, 1903 : 60, 177, pl. 11 fig. 18, pl. 12 figs 12, 32, pl. 13 figs 9, 15, 21, pl. 14 fig. 29; MORTENSEN, 1935; 157, pl. 3 figs 5-8, pl. 76 figs 17-19.

Eight specimens were collected during the MD03 expedition. They constitute the second record of this deep-sea species, and extend its geographical distribution to the South Indian Ocean. The 'Challenger' material originated from the Central Pacific Ocean, and off the coast of Chile.

Sterechinus diadema (Studer, 1876)

Echinus diadema Studer, 1876 : 456.
Sterechinus margaritaceus; MORTENSEN, 1903 : 101, 105, 177, pl. 19 figs 3, 20, 33.
Sterechinus diadema; DÖDERLEIN, 1903-1906 : 219, 225, pl. 27 fig. 5, pl. 35 fig. 1, pl. 47 figs 8, 10c; MORTENSEN, 1943 : 102, pl. 13 figs 3-4, pl. 19 figs 1-5, pl. 20 figs 4-5, pl. 56 figs 1-3.

S. diadema was dredged during the MD03, MD04, MD08 and 'Japonaise' expeditions around Marion, Crozet, Kerguelen and Heard islands. The specimens were identified on the basis of the diagnostic features given by MORTENSEN (1943). Mots of these features, observed in our specimens, vary in the direction of *S. neumayeri*. The general shape of the test varies from subconical to regularly hemispherical; the color of the cleaned test varies from whitish to brownish; the tube feet spicules are numerous or scarse; the outer corners of the valves of the globiferous pedicellariae may be produced. The question, whether *S. neumayeri* is really a distinct species from *S. diadema*, has been debated by CLARK (1925) and MORTENSEN (1943). CLARK (1925) considered them to be a single species, while MORTENSEN (1943) concluded that they have to be maintained as distinct, even thought he recognized that "none of these characters are absolutely constant" (p. 108). The range of variation shown in the present collection leads us to suspect that *S. diadema* and *S. neumayeri* are synonymous. A decision should be delayed until complementary non-morphological (i.e. molecular) arguments could be added to the discussion.

Plexechinus planus (Mironov, 1978)

Urechinus planus Mironov, 1978 : 216, pl. 1 figs 7, 8, pl. 2 figs 1, 2, 5, 6, pl. 3 figs 2, 4, 9.

The specimens from the Epos III collection are similar to those collected off South Tasmania during the 16th cruise of the R/V "D.M. Mendeleyev" (MIRONOV, 1978). However, considering the characteristics of the Epos III specimens and MIRONOV's original description, it is preferable to refer the species to the genus *Plexechinus* instead of *Urechinus* (fig. 2). The genera of Urechinidae are primarily based on the simultaneous occurrence of a subanal fasciole and an anal snout, and on the supra- or inframarginal position of the periproct. In fact, this distinction is rather confusing. The characters used for the distinction participate to progressive ontogenetic changes and are part of a morphological continuum between small species (i.e. *Plexechinus* spp.) presenting an anal snout, a conspicuous fasciole and a supramarginal periproct, and larger species (*Urechinus* spp.) lacking anal snout and fasciole, and presenting an inframarginal periproct. The limits fixed for each genus are arbitrary and unreliable and should be reconsidered, taking into account features other than those directly involved in ontogeny. The architecture of the plastronal area provides a more accurate generic distinction. Adults of *Plexechinus* generally display a discontinuous interambulacrum 5 that is interrupted by a pair of ambulacral plates joining on the midline, and the labrum is elongated;

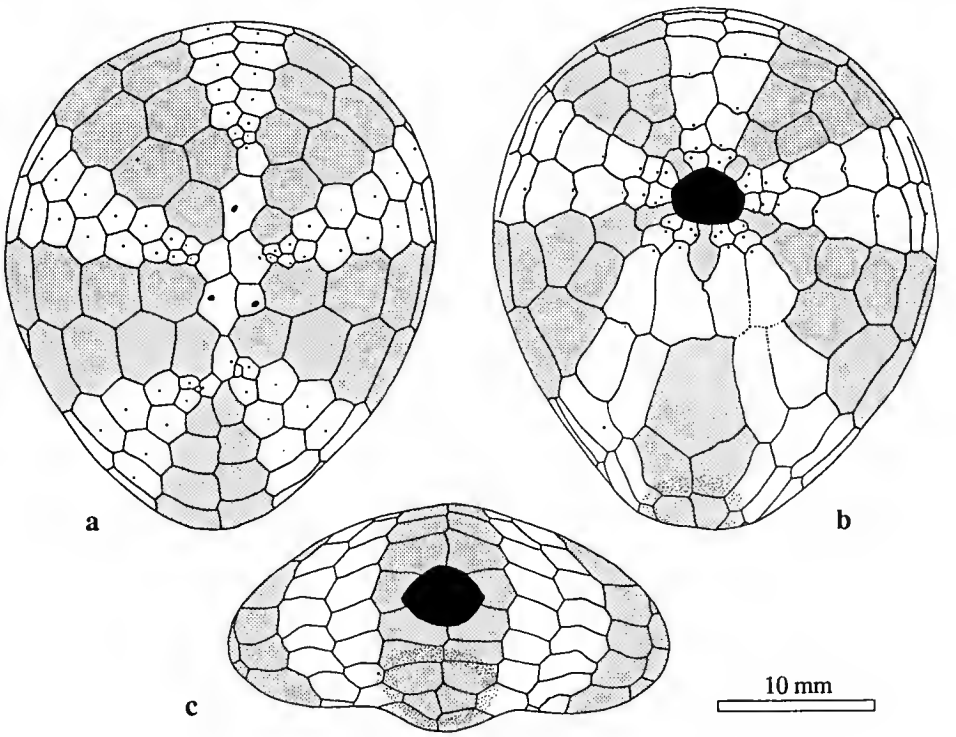

FIG. 2. — *Plexechinus planus*

occasionally interambulacrum 5 may be continuous, but with a narrow boundary between labrum and sternum (fig. 2b). *Urechinus* exhibits a classical plate pattern with a fully continuous interambulacrum 5. *U. aoteanus* McKnight (1976), reported as the only *Urechinus* species to present a discontinuous pattern, should be referred to *Plexechinus*. The tuberculation adds further arguments to this distinction : miliary tubercles form a regular dense coating, very apparent on the apical side in *Plexechinus*, while they are more scarcely distributed in *Urechinus*. Nevertheless even using these characters, the generic assignment remains ambiguous for some species, e.g. the brooding form *P. nordenskjoldi* (David & Mooi, 1990). Further large scale studies involving both ontogenetic and cladistic analyses are needed to clarify the relationships within the family.

Plexechinus aff. **cinctus** A. Agassiz, 1898

Plexechinus cinctus A. Agassiz, 1898 : 78, pl. 8 figs 3, 4; A. Agassiz, 1904 : 150, pl. 55 figs 3-5, pl. 58 figs 1-4, pl. 59, pl. 60 figs 1-3; Mortensen, 1950*b* : 119.

One broken specimen of MD03 from the Kerguelen region shows very puzzling characteristics and cannot be related with certainty to a known species. It is about 40 mm in length and its color is white purplish. Its general shape is elongated, with a triangularly grooved frontal ambulacrum resembling to some extent that of some extinct *Holaster*. A conspicuous subanal fasciole surrounds a smooth rostrum. The apical system is widely disjunct with separated bivium and trivium, and two gonopores open into a single genital plate. The interambulacrum 5 is interrupted by one pair of ambulacral plates between the labrum and the sternum. The miliary tuberculation forms a dense coating on the apical side. All those characters, excepts the sharp edged ambulacrum III, fit rather well the description of *P. cinctus*. This species is known only by two specimens from the Gulf of California at 1235 m depth, but it is the only one to which the MD03 specimen may be related although it has been found at a much shallower depth (585 m).

Pourtalesia aff. **hispida** A. Agassiz, 1879

Pourtalesia hispida A. Agassiz, 1879 : 204, pl. 205 figs 1-8, pl. 121 fig. 3; A. Agassiz, 1881 : 136, pl. 22 figs 6-19, pl. 39 figs 34, 36, pl. 41 figs 47, 48. Mortensen, 1950*b* : 149.

Specimens from Epos III resemble the two species of *Pourtalesia* which exhibit a short, but not elevated subanal rostrum (i.e. *P. aurorae* and *P. hispida*). Although they do not really fit either of these two species descriptions, they seem closer to *P. hispida* than to *P. aurorae*. The features shared with *P. hispida* are the vaulted lateral profile, the elongated general shape, and the serrated primary spines. On the other hand, the primary spines are not lined in regular horizontal rows and the ambital outline does not show parallel margins (they are curved as in *P. aurorae*). The position of the apex differs from the two above species; it is less anterior in the Epos III specimens. Owing to the relatively limited knowledge of the Antarctic species of *Pourtalesia* it is preferable to avoid describing a new species until more material becomes available (*P. aurorae* is based on 8 specimens described by Kœhler, 1926, and some fragments noted by Mironov, 1978; *P. hispida* is known from two type specimens, since destroyed,

described by A. AGASSIZ, 1879, and from the specimen described by KŒHLER, 1929). We refer the Epos III specimens to *P.* aff. *hispida*. The geographic distribution is rather different, the previously known specimens of *P. hispida* being reported from the South Indian Ocean (South Heard island).

Amphipneustes rostratus (Kœhler, 1926)

Antipneustes rostratus Kœhler, 1926 : 70, pl. 114 figs 1-6, pl. 115 figs 1, 3, 4, 6, pl. 116 figs 1-6, pl. 117 figs 1, 2, 6, 9, pl. 124 fig. 1.
Amphipneustes rostratus; MORTENSEN, 1951 : 268.

This species shows a wide range of individual variation and it was until now known only from a few specimens. *A. rostratus* is easily recognizable by its very large globiferous pedicellariae whose location remains detectable on naked tests by black spots. The posterior end of the test presents some variation as it may be vertically truncated with a marginal periproct, or rounded with an almost inframarginal periproct. The posterior interambulacrum may be depressed above the periproct. The ambital outline is usually more or less heart-shaped, but a few specimens have an almost oval ambitus. The sternum varies in width : it is wide and triangular in rounded specimens and narrow with parallel borders in more elongate specimens. The apical surface is covered by small tubercles densely distributed. Although *Amphipneustes* is characterized by the lack of fascioles, some of the Epos III *A. rostratus* may show a marginal fasciole, and one specimen has a short portion of a peripetalous fasciole.

Brachysternaster chesheri Larrain, 1985

Brachysternaster chesheri Larrain, 1985 : 121, figs 1-3.

The numerous specimens of *Brachysternaster* collected during Epos III expedition allow us to add some comments about the range of variation of this species. All the Epos III specimens fit closely to LARRAIN's description of the type and the two paratypes in the general shape of the test and the plate architecture. However, two "forms" can be distinguished : (1) large (ca. 75 mm in length) purplish specimens with scarce, evenly distributed primary tubercles; (2) smaller (ca. 55 mm in length) yellowish specimens with a more dense canopy of primaries. Both forms show on the apical side numerous scars which result from the loss of primary tubercles (similar to those observed in other irregular echinoids, DAVID & NÉRAUDEAU, 1989). Statistical comparisons of some shape parameters show no morphological differences between the two forms.

Parapneustes abatoides (Clark, 1925)
(Pl. V, 3-4)

Pericosmus abatoides H. L. Clark, 1925 : 199, pl. 11 figs 4-6.
Tripylus (*Parapneustes*) *abatoides*; MORTENSEN, 1951 : 279.

KŒHLER (1912*b*) created the genus *Parapneustes* for two new species, *P. cordatus* and *P. reductus*, without proposing a type species. On the basis of the two specimens available (i.e. the

two holotypes) KŒHLER noted that *P. cordatus* possesses only a peripetalous fasciole, while *P. reductus* possesses both a peripetalous and a marginal fasciole. CLARK (1925) described a new species, *Pericosmus abatoides*, which also possesses a peripetalous and a marginal fasciole. Later, he referred the species to the Schizasteridae, stating that "it is probably related to *Abatus* and will ultimately have to be made the type of a new genus" (1932 : 218). Finally, MORTENSEN (1951) studied specimens of *Parapneustes cordatus* collected by the "Discovery", and reported the occurrence of a latero-subanal fasciole (not observed by KŒHLER on the type specimen). He then referred *cordatus* to *Tripylus* (*Parapneustes*), restricting *Parapneustes* as a subgenus. He also placed KŒHLER's and CLARK's species (*reductus* and *abatoides*, respectively) in *Tripylus* (*Parapneustes*). He based his decision on a reinterpretation of the fascioles,

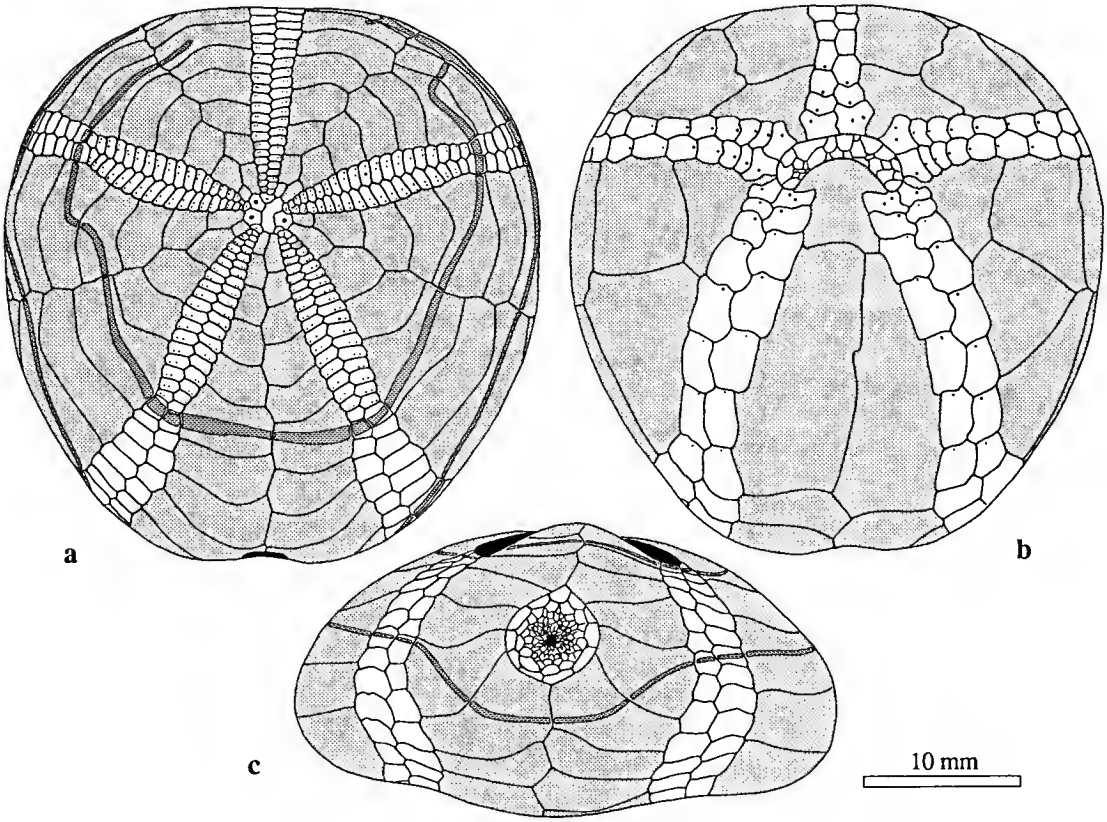

FIG. 3. — *Parapneustes abatoides*.

considering that both KŒHLER and CLARK's "marginal fasciole" was in fact the latero-subanal fasciole. MORTENSEN had drastically revised KŒHLER and CLARK's descriptions without having any specimen in hand. The Epos III specimens perfectly fit the species *P. abatoides* (fig. 3). They corroborate CLARK's description and cost doubt on MORTENSEN's interpretations. They possess a complete marginal fasciole and a peripetalous fasciole which

never crosses the anterior ambulacrum (fig. 3a). In some specimens, the peripetalous fasciole turns backwards for a more or less short distance, thus appearing double on the anterior interambulacra (a characteristic already quoted by CLARK). Similarly, the illustrations of the species *reductus* given by KŒHLER clearly show the presence of a marginal fasciole. Owing to these observations it is preferable to refer *reductus* and *abatoides* to *Parapneustes* and to retain *cordatus* in *Tripylus*. The proposed taxonomic position for *P. abatoides* is reinforced by the length of the latero-anterior petals, which reach the peripetalous fasciole. In complete revision of the brooding schizasterids, we would suggest that : (1) the genus *Parapneustes* is valid, and includes *P. abatoides* and *P. reductus*; (2) the genus *Tripylus* includes *T. cordatus, T. excavatus* and *T. beatriceae*; (3) the genus *Tripylus* could be close to *Abatus*, because of both possess a latero-subanal fasciole.

Delopatagus aff. **brucei** Kœhler, 1907

Delopatagus brucei Kœhler, 1907 : 147; KŒHLER, 1908 : 622, pl. 15 figs 130-135; MORTENSEN, 1950*b* : 252.

The morphological characters of the two broken specimens collected during the Epos III Expedition are those given by KŒHLER in 1908. The Epos III specimens show a minor difference — their latero-posterior petals are not shorter than the anterior ones. This is why we identify them as *D.* aff. *brucei*. Recent RNA-sequencing studies reveal that the Epos III specimens of *Delopatagus* are very close to *Amphipneustes* (Féral & Derelle, 1991). These data must be taken into account in reconsidering the taxonomic position of the genus *Delopatagus* as far as the Asterostomatidae constitutes an heterogenous polyphyletic group (FISHER, 1966). We suggest that *Delopatagus* belongs to the Schizasteridae, close to *Amphipneustes*. Like *Amphipneustes, Delopatagus* has no fascioles. Moreover, additional specimens held at the Smithsonian Institution (USNM E11063, E11274, E11275, E11286) have depressed petals that house juveniles. This indicates that *D. brucei* is a brooding species. This is strong evidence in supporting the idea that *Delopatagus* belongs in the Schizasteridae, the only brooding family in the spatangoids.

DISCUSSION

1. **Geographical distribution**

Two circumpolar regions, the Antarctic and the Subantarctic Regions are involved here. The Antarctic Region corresponds to an area extending from the shore of the Antarctic Continent to the Antarctic Convergence (fig. 4); it includes a large series of islands, namely, the South Shetlands, South Orkneys, the South Sandwich, South Georgia and Bouvet islands. As defined by PAWSON (1969), the Subantarctic Region covers a vast oceanic area south of the Subtropical Convergence (except that the limits of this region on the two sides of South America are not yet defined), and the shallow waters of the tip of South America (fig. 4); it includes Kerguelen, Heard and Macquarie Islands but not the southern of New Zealand although this lies within the limits of the Subtropical Convergence. Both regions are

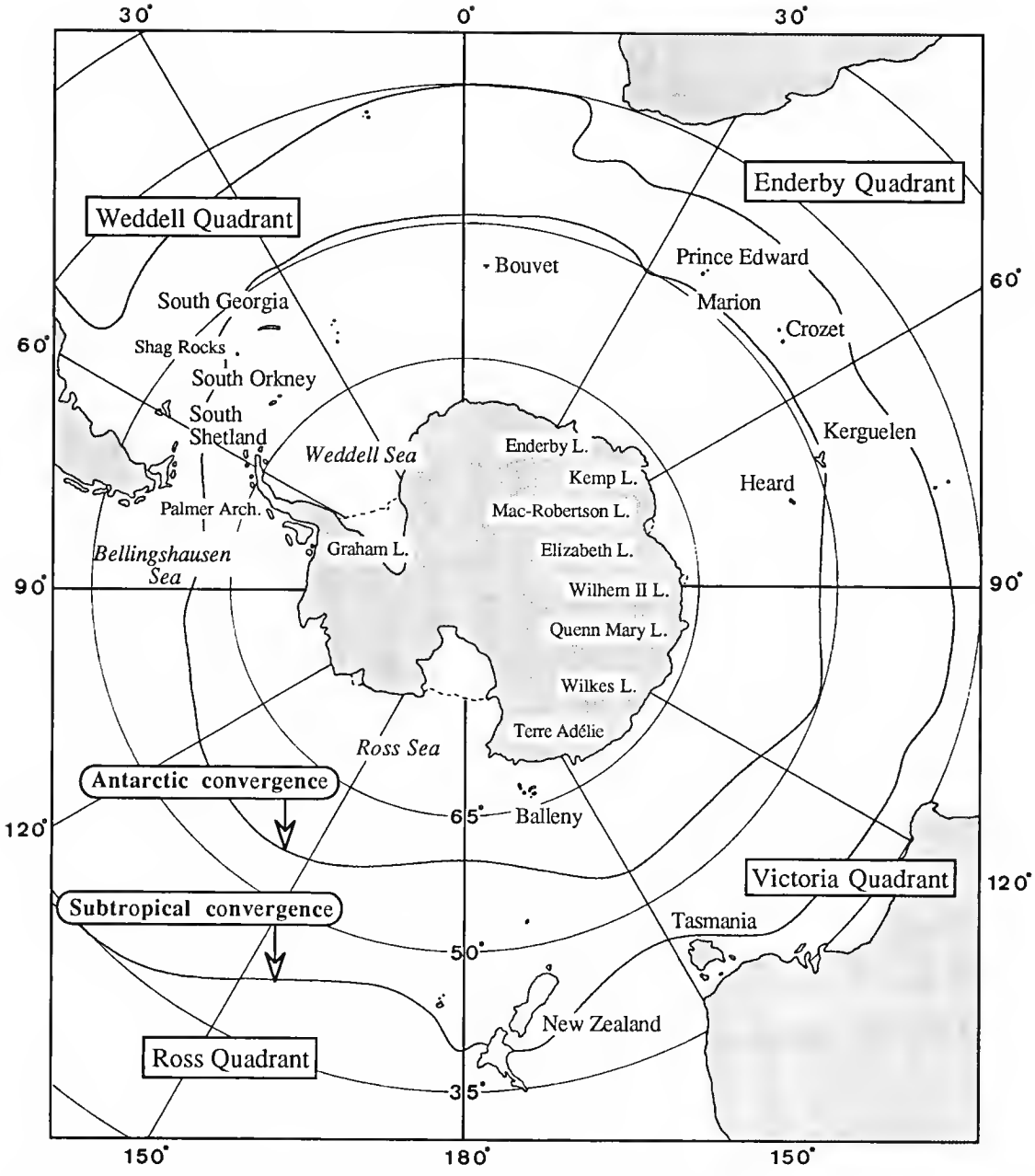

FIG. 4. — The Antarctic and Subantarctic regions and their biogeographical divisions (modified after PAWSON. 1969).

subdivided into four geographical quadrants : the Weddell, the Enderby, the Victoria and the Ross quadrants that respectively correspond to an American, an African, an Australian and a Pacific zone; these quadrants are identified for convenience; they have no biological significance. The biogeographic divisions used further in this discusion are those proposed by PAWSON (1969) : the Magellanic Subregion or Province, the Tristan da Cunha District and the Kerguelen Subregion or Province, for the Subantarctic region; the Continental or High Antarctic Subregion or Province, the extension of Continental Subregion of Province, the Scotia Subregion and the South Georgia District, for the Antarctic Region.

As already mentioned by PAWSON (1969) and by DELL (1972), over 50 families of echinoids are known but only six of them, namely, the Cidaridae, the Echinidae, the Arbaciidae, the Urechinidae, the Pourtalesiidae, and the Schizasteridae, occur in the Antarctic-Subantarctic Regions. A seventh family, the Echinothuriidae, can be added to this list, as specimens of *Kamptosoma asterias* were collected south of Heard Island during the MD03 Expedition. Very characteristic are the absence of the vast assemblage of regular non-cidaroid echinoids (apart from two genera, *Sterechinus* and *Kamptosoma*), and the diversity of two families, the Schizasteridae and the Cidaridae (within which all the Antarctic-Subantarctic species belong to one subfamily, the Ctenocidarinae) (PAWSON, 1969). The geographic distributions of the species collected are summarized in Table 6. There are several new range extensions. Wide latitudinal extensions, i.e., from one zone to another, are observed for five species : *Kamptosoma asterias* which extends from the Temperate to the Subantarctic Zone, *Ctenocidaris nutrix longispina, Urechinus wyvilli, Plexechinus planus*, and *Brisaster kerguelensis* which extend from the Subantarctic to the Antarctic Zone. Longitudinal extensions are observed within the Antarctic Zone, the Subantarctic Zone or both simultaneously. Within the Antarctic Zone, four species previously unreported in the Weddell Quadrant were collected in the Weddell Sea : *Amphipneustes rostratus* (known from the Victoria Quadrant), *Homalocidaris gigantea* (known from the Ross and the Victoria Quadrants), *Pourtalesia hispida* (known from the Victoria and Enderby Quadrants), *Amphipneustes bifidus* (known from the Enderby Quadrant), and *Parapneustes abatoides* (known from the Ross Quadrant). Nine other species (*Ctenocidaris speciosa, Notocidaris gaussensis, Notocidaris mortenseni, Sterechinus antarcticus, Plexechinus nordenskjoldi, Abatus cavernosus, Amphipneustes lorioli, Amphipneustes similis* and *Brachysternaster chesheri*), already reported in the Weddell Quadrant in the Bellingshausen Sea or along the Antarctic peninsula are now known to occur in the east part of the Weddell Sea. Within the Subantarctic Zone, two species extend longitudinally : in the Enderby Quadrant, *Brisaster kerguelensis*, known from Kerguelen and Bouvet Islands, reaches the Crozet and Heard Islands; *Tripylaster philippi*, known in the Weddell Quadrant, extends to the Enderby Quadrant (Marion and Prince Edward Islands). One species, *Sterechinus neumayeri*, known in both Antarctic and Subantarctic Zones from three Quadrants extends in both Zones simultaneously to the fourth Quadrant (Enderby Quadrant).

TABLE 6. — Geographical distribution of the collected species (expanded areas, corresponding to this paper, are in bold-fact types).

SPECIES	Antarctic (AZ), Subantarctic (SAZ) or Temperate (TZ) zones	LOCALITIES (W.Q. = Weddel quadrant, E.Q. = Enderby quadrant V.Q. = Victoria quadrant, R.Q. = Ross quadrant)	DATA SOURCES
Aporocidaris antarctica	SAZ + AZ	E.Q. + V.Q. (off Elizabeth to Queen Mary Lands, Kerguelen Isl.)	BELL 1908, 1917; KŒHLER 1912*a*, *b*; MORTENSEN 1928*b*; PAWSON 1969
Ctenocidaris nutrix	SAZ + AZ	E.Q. (off Antarctic coast, Kerguelen, Crozet, Heard Isl.)	AGASSIZ 1881; DÖDERLEIN 1903-06; GUILLE 1977*b*; KŒHLER, 1912 *a*, *b*. 1917; MORTENSEN 1903, 1909, 1928*b*; PAWSON, 1969; STUDER 1876, 1880; WYV. THOMPSON 1876, 1877
Ctenocidaris nutrix longispina	SAZ	E.Q. (Heard Isl.) + **W.Q. (Weddel Sea)**	MORTENSEN 1928*a*, *b*
Ctenocidaris perrieri	AZ	W.Q. (South Shetlands Isl., Palmer Arch.,Bellingshausen Sea, Weddell Sea) + V.Q. (Balleny Isl.) + R.Q. (Ross Sea)	BELL 1908, 1917; KŒHLER 1912*a*, *b*; MORTENSEN 1925, 1928*b*; PAWSON, 1969; FELL 1976
Ctenocidaris speciosa	SAZ + AZ	V.Q. (Coulman, Balleny Isl.) + W.Q. (off Graham Land, Palmer Arch., South Georgia South Orkneys, South Shetlands Isl., Shag Rocks, off Tierra del Fuego, **Weddell Sea)**	BERNASCONI 1953; KŒHLER 1926; MORTENSEN 1910, 1928*a*, *b*, 1936; PAWSON 1969; FELL 1976
Ctenocidaris spinosa	AZ	V.Q. (off Queen Mary Land) + W.Q. (Weddell Sea)	KŒHLER 1926; MORTENSEN 1928*b*; PAWSON 1969; FELL 1976
Homalocidaris gigantea	AZ	R.Q. (Ross Sea) + V.Q. (off Victoria Land) + **W.Q. (Weddel Sea)**	CLARK 1925; MC KNIGHT 1976; MORTENSEN 1928*b*, 1950*a*; PAWSON 1969
Notocidaris gaussensis	AZ	R.Q. + W.Q. (South Shetlands Isl., Bellingshausen Sea, **Weddell Sea)**	KŒHLER 1912*b*; MORTENSEN 1909, 1928*b*, 1950*a*; PAWSON 1969; FELL 1976
Notocidaris mortenseni	AZ	E.Q. (off Kemp Land to Wilhem II Land) + W.Q. (South Shetlands Isl., **Weddell Sea)**	BERNASCONI 1953; DÖDERLEIN 1903-06; KŒHLER 1900, 1901; MORTENSEN 1909, 1928*b*; PAWSON 1969; FELL 1976
Kamptosoma asterias	TZ + AZ	off coast of Chile (33°31′S) + **E.Q. (South Heard Isl.)**	A. AGASSIZ 1881, 1904; MORTENSEN 1903, 1935
Sterechinus agassizi	SAZ + AZ	W.Q. (South Georgia, Falklands Isl.), South Atlantic (American coast up to 46°14′S)	AGASSIZ 1872-74; BERNASCONI 1953; KŒHLER 1912*b*, MEISSNER 1900; MORTENSEN 1909, 1943; PAWSON 1969

Sterechinus antarcticus	AZ	W.Q. (South Georgia, South Shetlands Isl., Palmer Arch., off Graham Land, **Weddell Sea**) + V.Q. (Balleny Isl.) + E.Q. (Kemp Land to Mac-Robertson Land)	BERNASCONI 1953; KŒHLER 1901, 1912*b*, 1926; MC KNIGHT 1976; MORTENSEN 1903, 1909, 1936, 1943, 1950*a*; PAWSON 1969
Sterechinus neumayeri	SAZ + AZ	V.Q. (off Terre Adélie, Balleny Isl.) + W.Q. (Palmer Arch., South Orkneys, South Shetlands, South Georgia, South Patagonia Isl.) + R.Q. (Ross Sea) + **E.Q. (Prince Edward, Marion, Crozet, Kerguelen Isl.)**	ARNAUD 1965; BERNASCONI 1953; DÖDERLEIN 1903-06; GRIEG 1929*a, b*; KŒHLER 1908, 1912b, 1926; MC KNIGHT 1976; MORTENSEN 1903, 1909, 1910, 1925, 1936, 1943, 1950*a*; PAWSON 1969
Plexechinus planus	SAZ + AZ	V.Q. (44°06′S-145°56′E) + **W.Q. (Weddell Sea)**	MIRONOV 1978
Plexechinus nordenskjoldi	AZ	E.Q. (off Enderby to Mac-Robertson Lands) W.Q. (South Georgia Isl., Antarctic, **Weddell Sea**)	BERNASCONI 1953; KŒHLER 1912*b*; MORTENSEN 1905, 1909, 1910, 1936, 1950*a*
Urechinus wyvilli	SAZ + AZ	Subantarctic Sea (E.Q., V.Q., R.Q., W.Q.) + off Pacific coast of Chile (up to 33° S) + **W.Q. (Weddell Sea)**	A. AGASSIZ 1879, 1881; KŒHLER 1908; MORTENSEN 1907, 1909, 1950*b*; USNM collections
Urechinus mortenseni	AZ	W.Q. (off Graham Land)	DAVID & MOOI 1990
Pourtalesia hispida	SAZ + AZ	E.Q. (extreme South of Indian ocean) + V.Q. (off Queen Mary Land) + **W.Q. (Weddell Sea)**	A. AGASSIZ 1881; KŒHLER 1912*b*, 1926; MORTENSEN 1907, 1909, 1950*b*
Abatus cavernosus	SAZ + AZ	W.Q. (South America 36° S to South Georgia, Palmer Arch., **Weddell Sea**) + V.Q. Terre Adélie) + E.Q. (Kerguelen Isl., Heard Isl.)	AGASSIZ 1881; BERNASCONI 1953; DÖDERLEIN 1903-06; GRIEG 1929*a, b*, KŒHLER 1908, 1912b, 1926; MEISSNER 1900; Mortensen 1909, 1910, 1936, 1950*a*, 1951; PAWSON 1969; PHILIPPI 1845; STUDER 1876, 1880
Abatus cordatus	SAZ	E.Q. (Kerguelen Isl.)	A. AGASSIZ 1881; CHERBONNIER & GUILLE 1975; DÖDERLEIN 1903-06; GUILLE 1977*b*; KŒHLER 1912*b*, 1917; MORTENSEN 1909, 1936, 1950*a*, 1951; PAWSON 1969; SMITH 1879; STUDER 1876, 1880; VERRILL 1876
Amphipneustes bifidus	AZ	E.Q. (Enderby Land, Kemp Land) + **W.Q. (Weddell Sea)**	MORTENSEN 1950*a*; PAWSON 1969
Amphipneustes lorioli	AZ	W.Q. (Palmer Arch., Bellingshausen Sea, **Weddell Sea**) + V.Q. (between Queen Mary and Wilkes Lands)	BERNASCONI 1953; KŒHLER 1900, 1901, 1912*a, b*; MORTENSEN 1909, 1910, 1936, 1950*a*, 1951; PAWSON 1969

Amphipneustes rostratus	AZ	V.Q. (off Queen Mary Land to Terre Adélie) + **W.Q. (Weddell Sea)**	MORTENSEN 1951; PAWSON 1969
Amphipneustes similis	AZ	W.Q. (Palmer Arch., **Weddell Sea**)	BERNASCONI 1953; MORTENSEN 1936, 1951; PAWSON 1969
Brachysternaster chesheri	AZ	W.Q. (South Shetlands Isl., **Weddell Sea**)	LARRAIN 1985
Brisaster kerguelensis	SAZ + AZ	E.Q. (Kerguelen, Bouvet, **Crozet, Heard Isl.**)	DÖDERLEIN 1903-06; MORTENSEN 1950*a*, 1951; PAWSON 1969
Delopatagus brucei	AZ	W.Q. (South Georgia Isl., **Weddell Sea**)	KŒHLER 1907, 1908, 1912*b*; MORTENSEN 1909, 1950*b*
Parapneustes abatoides	AZ	R.Q. (Ross Sea) + **W.Q. (Weddell Sea)**	CLARK 1925; MORTENSEN 1951
Tripylaster philippi	SAZ + AZ	South America 35°S (Rio de la Plata) to the Fuegian coast + W.Q. (South Georgia Isl.) + **E.Q. (Prince Edward, Marion Isl.)**	BERNASCONI 1953; DÖDERLEIN 1903-06; KŒHLER 1912*b*; MEISSNER 1900; MORTENSEN 1907, 1909, 1910, 1936, 1951, 1952; PAWSON 1969; STUDER 1880

Three major patterns of distribution can now be identified among the echinoid genera :

1 — A circumpolar distribution in the Antarctic Zone only for six genera (*Homalocidaris, Notocidaris, Amphipneustes, Brachysternaster, Parapneustes, Delopatagus*).

2 — A Circumpolar distribution in the Antarctic Zone, but with representatives in the Magellanic and in the Kerguelen Provinces (*Ctenocidaris, Sterechinus*), or with representatives in the above mentioned Provinces and in the southern coastal waters of America for two other genera (*Abatus* which occurs up to 36° S off Argentina, and *Tripylaster* which occurs up to 41°50 S off Chile and up to 35° S off Argentina).

3 — A circumpolar distribution in the Antarctic and Subantarctic Zones with representatives in more northern areas : five genera (*Aporocidaris, Brisaster, Pourtalesia, Plexechinus, Urechinus*. These four last genera are deep-sea forms).

A deep-sea occurrence in the Subantarctic Zone is observed for *Kamptosoma*, a genus already known from more northern areas.

According to PAWSON (1969), fifteen genera (*Ctenocidaris, Rhynchocidaris, Homalocidaris, Aporocidaris, Notocidaris, Sterechinus, Abatus, Amphipneustes, Brisaster, Tripylus, Tripylaster, Delopatagus, Urechinus, Pourtalesia* and *Plexechinus*) have been collected in the Antarctic Zone. The total is now seventeen genera, with *Brachysternaster* described in 1985 by LARRAIN and with *Parapneustes* revalidated in the present work. Two of the genera mentioned by PAWSON (1969), i.e. *Rhynchocidaris* and *Tripylus*, were not collected during the expeditions reported here. Of the seventeen genera now known to occur in the Antarctic Zone, seven (see pattern 1 + *Rhynchocidaris*) are restricted to the Antarctic Zone, five (see pattern 2 + *Tripylus*) are restricted to the Antarctic-Subantarctic Zones and five occur elsewhere in the world. The proportion of endemic genera in the Antarctic Zone calculated from our data is higher than that mentioned by DELL (1972) (41 % versus 25 %).

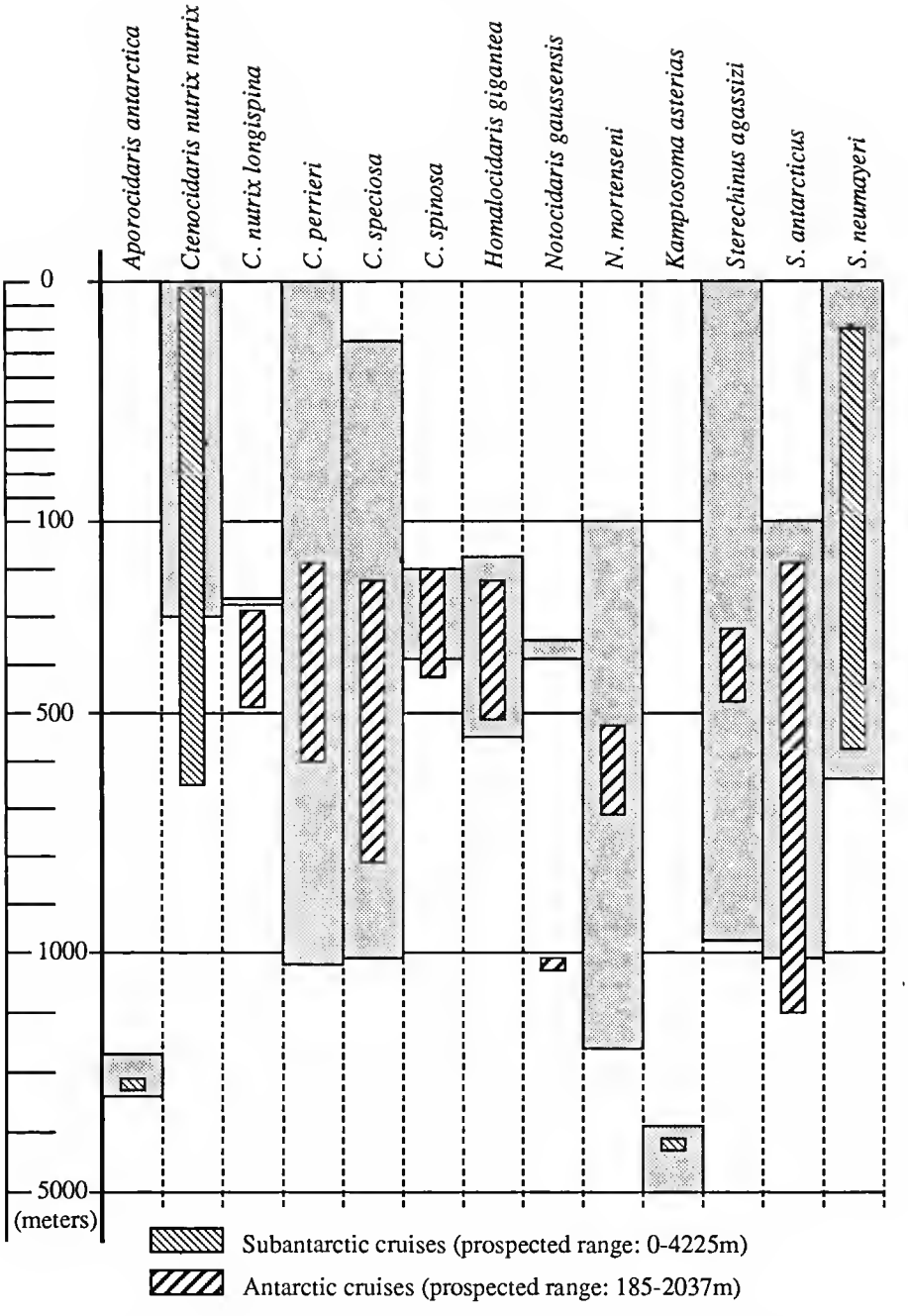

FIG. 5. — Bathymetrical distribution of the collected species (regular echinoids).

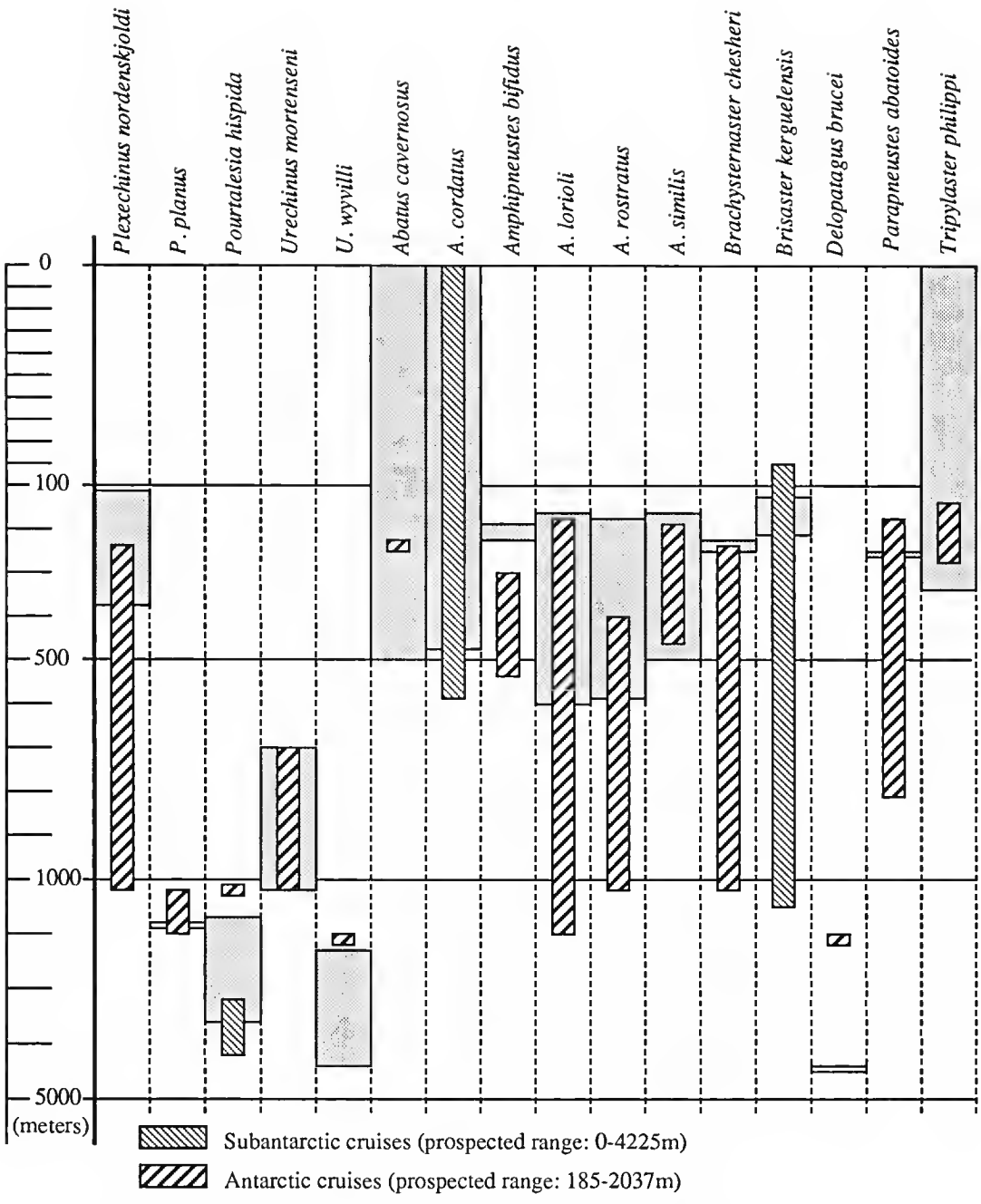

FIG. 6. — Bathymetrical distribution of the collected species (irregular echinoids).

2. Bathymetrical distribution

The continental shelf around Antarctica is narrow, except in the two embayments of the Ross Sea and the Weddell Sea (DELL, 1972). Its outer limit generally lies between 400 and 600 m deep, but it reaches 800 m in the Ross Sea. The continental slope ends at depths of 3000 m. From there three main basins are arranged around the continent : an Atlantic-Indian-Antarctic basin, an Eastern Indian-Antarctic basin and a Pacific-Antarctic basin. The northern limits of each basin correspond to major ridges (crests located at depths less than 3000 m) arranged in a more or less circumpolar fashion (DELL, 1972). Figures 5 and 6 summarize the bathymetrical distribution of the species collected and displays a comparison between the previously known bathymetric distributions and the distributions recorded in the present work. We can expand downward the bathymetric range of several species. Two species (*Ctenocidaris nutrix longispina*, and *Amphipneustes bifidus*) reach the outer edge of the continental shelf in the Weddell Sea. Two other species reach the epibathyal zone (*Ctenocidaris nutrix nutrix* in the Kerguelen area, and *Parapneustes abatoides* in the Weddell Sea). The range of five species is expanded from the continental shell to the bathyal zone : *Notocidaris gaussensis, Plexechinus nordenskjoldi, Amphipneustes rostratus*, and *Brachysternaster chesheri* in the Weddell Sea ; *Brisaster kerguelensis* from the MD expeditions. One species, *Amphipneustes lorioli*, previously known to occur down to 600 m, reaches more than 2000 m in the Weddell Sea.

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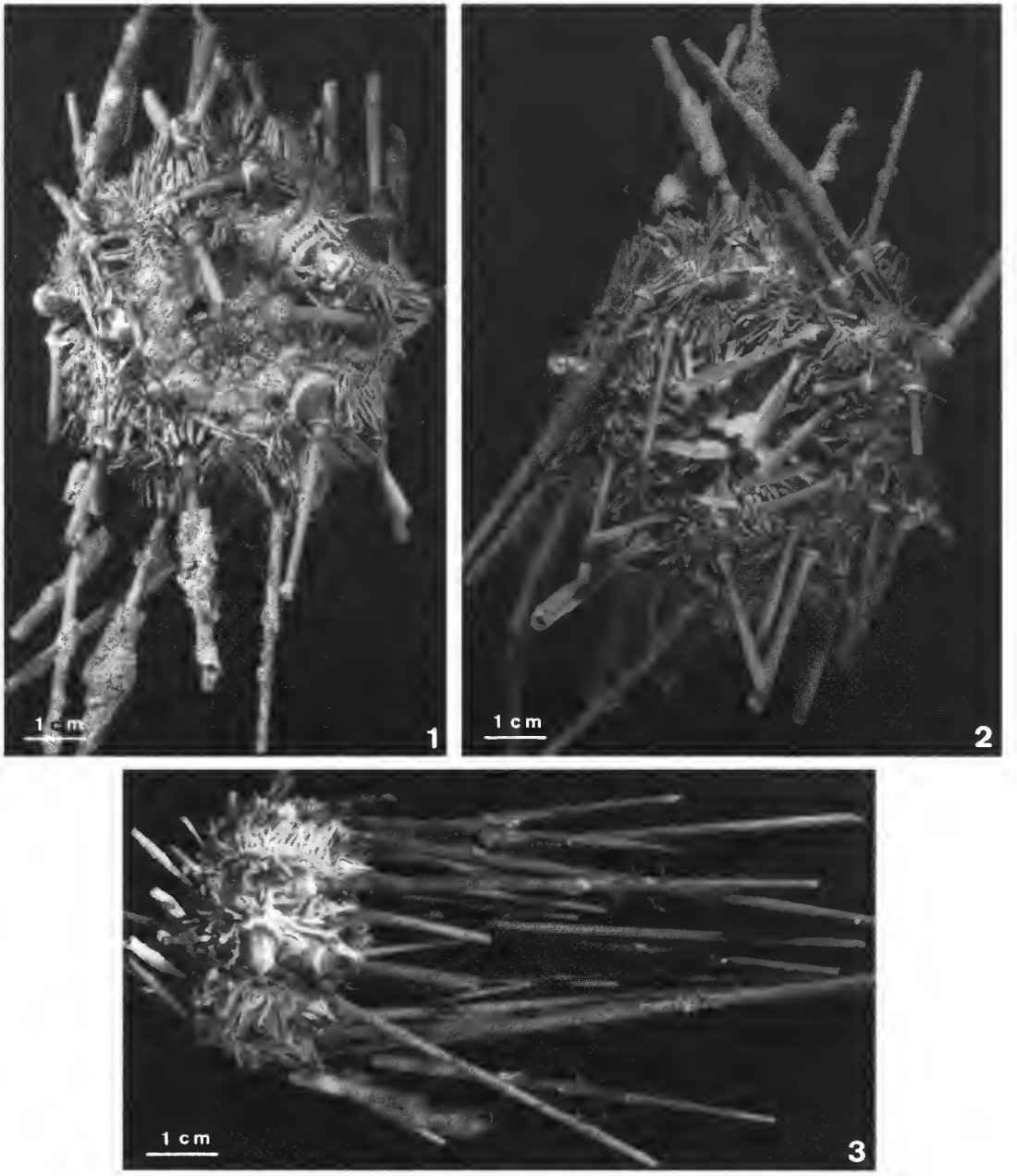

PLATE I. — *Ctenocidaris nutrix longispina* : apical view (1), oral view (2), lateral view (3).

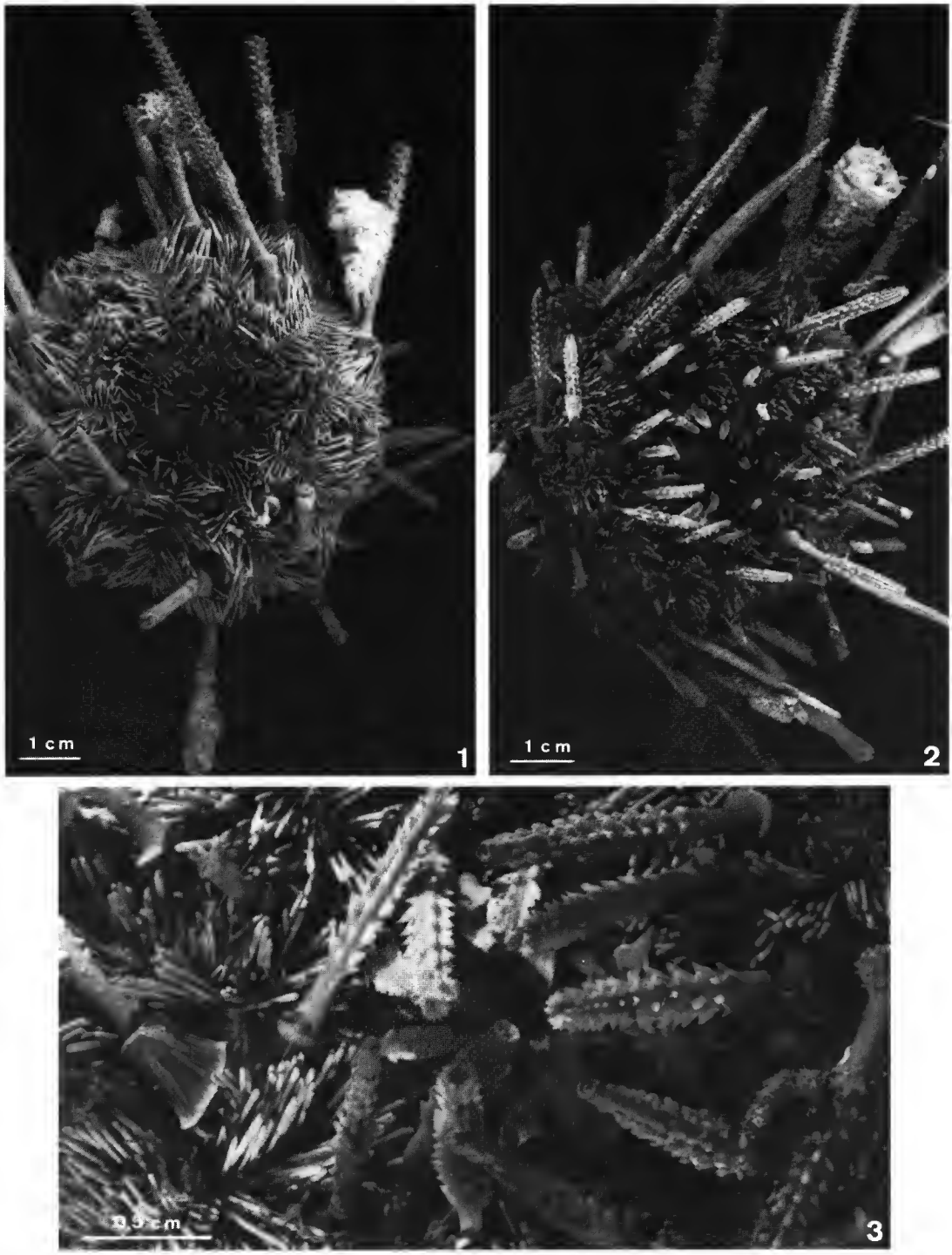

PLATE II. — *Ctenocidaris perrieri* : apical view (1), oral view (2), peri-oral area (3).

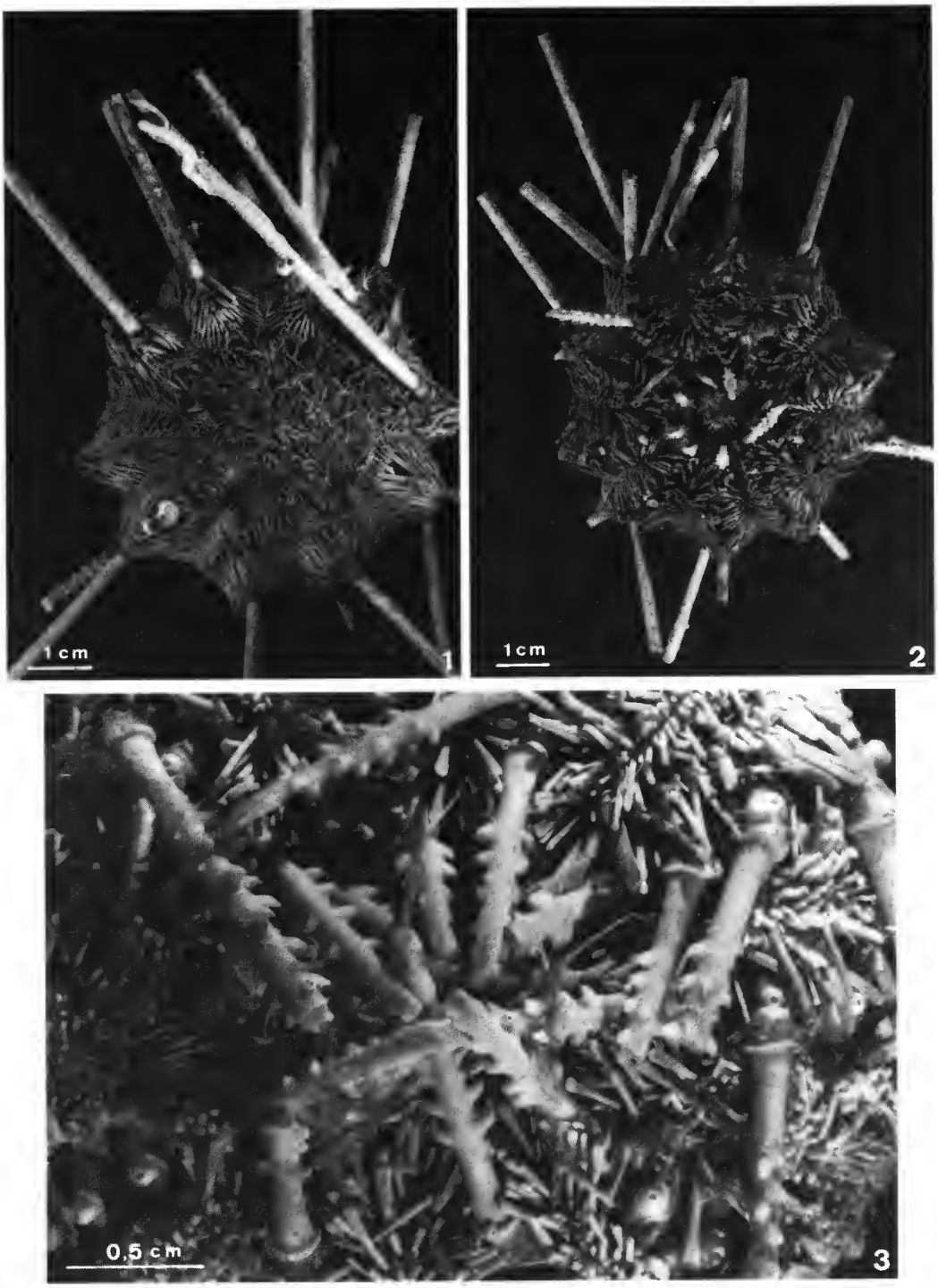

PLATE III. — *Ctenocidaris speciosa* : apical view (1), oral view (2), peri-oral area (3).

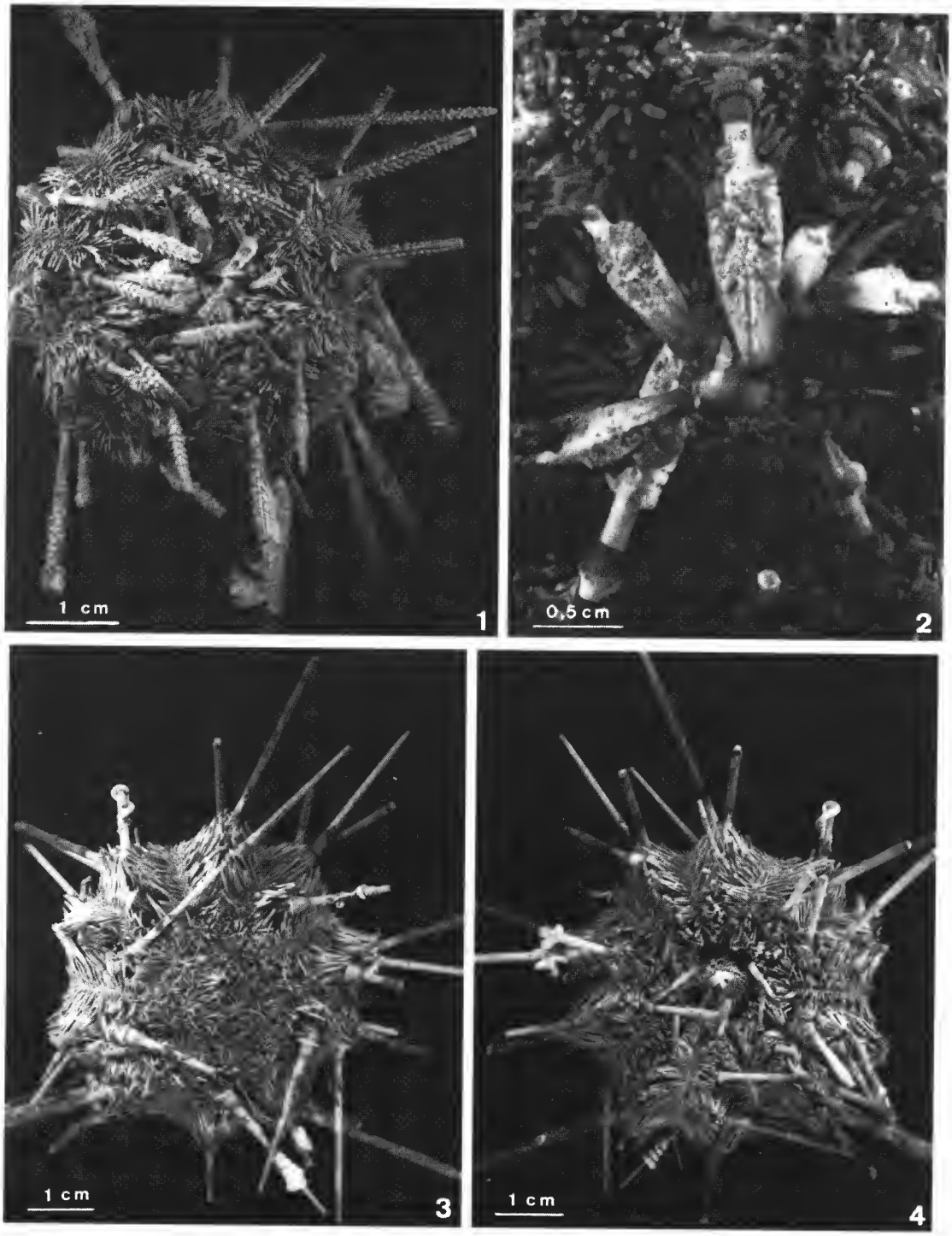

PLATE IV. — *Ctenocidaris spinosa* ; oral view (1), peri-oral area (2). *Homalocidaris gigantea* : apical view (3), oral view (4)).

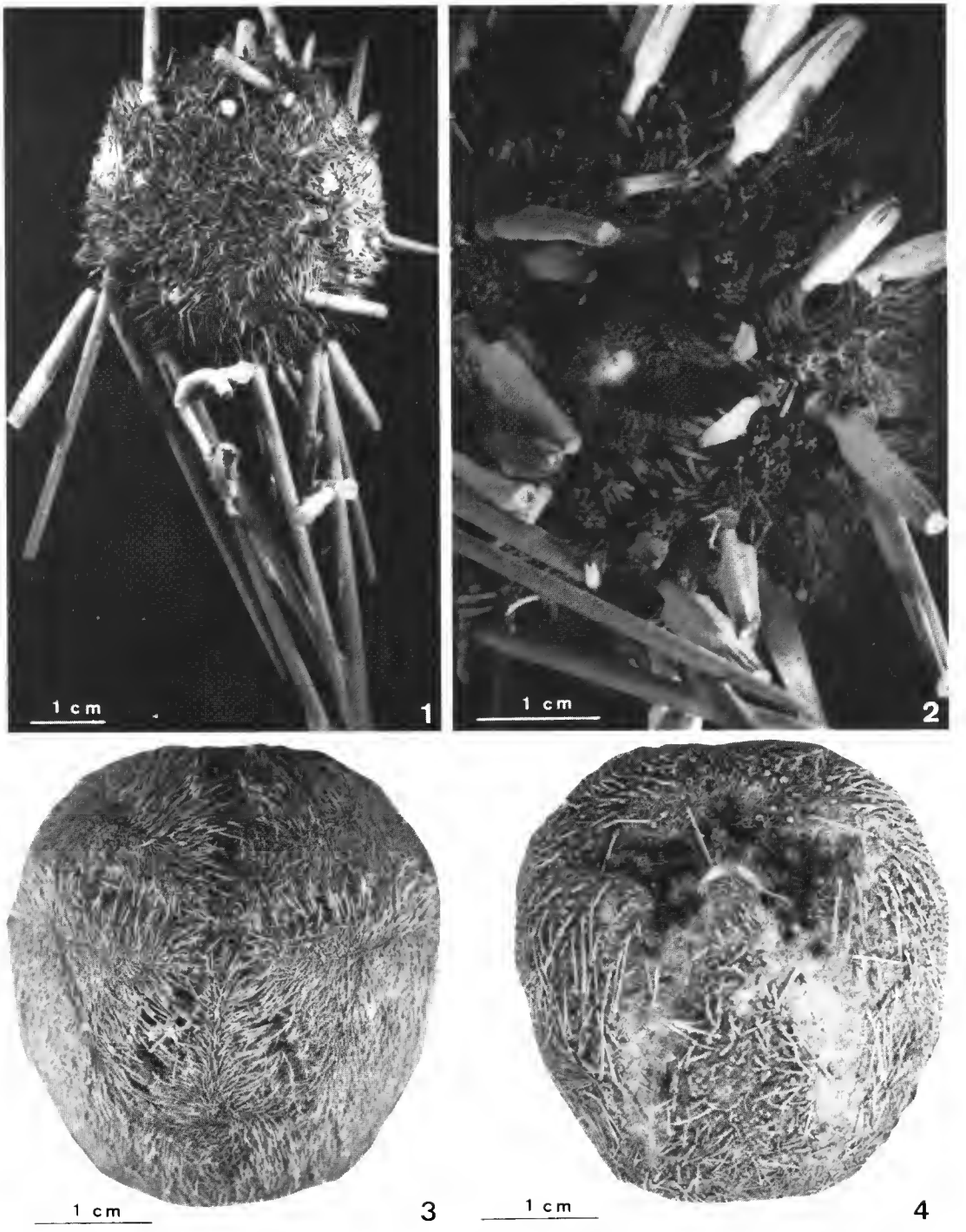

PLATE V. — *Notocidaris gaussensis* : apical view (1), peri-oral area (2). *Parapneustes abatoides* : apical view (3), oral view (4).

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section A, n° 2 : 443-448.

Neovermilia anoperculata, nouvelle espèce bathyale de Nouvelle-Calédonie (Polychaeta, Serpulidae)

par Jean-Paul LECHAPT

Résumé. — *Neovermilia anoperculata* sp. nov. est décrite à partir du matériel récolté au cours de la campagne « Biocal ». Le principal caractère distinguant les individus observés des autres espèces du genre est l'absence d'opercule.

Abstract. — *Neovermilia anoperculata* sp. nov. is described from material collected during the bathy-abyssal cruise "Biocal" off New Caledonia (Pacific Ocean). The chief distinguish character of these specimens is the lack of operculum.

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La campagne « Biocal » a eu lieu en 1985, à bord du « Jean Charcot », au large de la Nouvelle-Calédonie. Parmi les Serpulidae récoltés, nous avons pu identifier quelques individus appartenant au genre *Neovermilia* défini par DAY (1961). Ce genre possède des soies thoraciques simples, capillaires, semblables à celles du genre *Vermiliopsis*, mais il n'y a pas de soies en faux du type « *Apomatus* ». L'absence d'opercule chez tous les spécimens examinés est considérée comme un caractère spécifique et nous a conduit à décrire cette nouvelle forme bathyale.

Le matériel-type est déposé au Muséum national d'Histoire naturelle, Paris (MNHN).

Neovermilia anoperculata n. sp.

MATÉRIEL EXAMINÉ : Station DW 51 (31/08/85), 23°05′ S-167°44′ E-167°45′ E, 680-700 m, 2 individus (holotype et un spécimen incomplet); station CP 108 (09/09/85), 22°02′ S-167°05′ E-167°06′ E, 335 m, 10 individus (paratypes).

DESCRIPTION

L'holotype de la station DW 51 (MNHN UC 163) mesure 10 mm de longueur, dont 4 mm pour le panache branchial. Celui-ci est constitué de 33 filaments (16 d'un côté, 17 de l'autre) dont les extrémités s'enroulent sur elles-mêmes ce qui leur donne un aspect renflé. Il n'y a pas d'opercule. La membrane thoracique dépasse le 7e et dernier sétigère. L'abdomen comprend 30 à 40 sétigères (fig. 1).

FIG. 1. — *Neovermilia anoperculata* sp. nov. : individu entier, face ventrale.

Les soies du premier sétigère thoracique sont toutes capillaires et nettement frangées de petites soies (pl. I, 1-2). Les soies des segments thoraciques suivants sont finement denticulées (pl. I, 3-4); elles sont lisses à leur base, les denticulations n'apparaissant qu'aux 2/5 de leur longueur et sur un seul côté de la soie ce qui leur confère une apparence limbée à faible grossissement. Il n'y a pas de soies en faux du type « *Apomatus* ».

Les uncini thoraciques présentent une rangée simple de 5 dents (pl. II, 1); les rangées d'uncini se rejoignent presque à la face ventrale des derniers segments thoraciques (fig. 1).

Les segments abdominaux possèdent des soies géniculées et denticulées (pl. II, 2) et des uncini présentant vers l'avant 4 à 6 dents disposées en une seule rangée et vers l'apex une double rangée de 2 à 3 dents (pl. II, 3).

Les tubes sont blancs, lisses, solides, les plus gros ayant 3 mm de diamètre, ceux-ci présentant quelques bourrelets plus ou moins saillants à l'extrémité antérieure (pl. III, 1-2).

Les dix paratypes de la station CP 108 (MNHN BOCAL A915) mesurent de 1,2 mm à 5 mm de longueur, le panache branchial non compris. Aucun ne porte d'opercule. Les paratypes possèdent les mêmes types de soies et d'uncini que l'holotype. L'individu incomplet de la station DW 51 n'est pas inclus dans la série des types.

REMARQUES

Les espèces de *Neovermilia* décrites jusqu'à présent possèdent un opercule : *N. capensis* Day, 1961, de l'Afrique du Sud (DAY, 1967); *N. falcigera* (Roule, 1898), de l'Atlantique (SOUTHWARD, 1963) et de l'océan Indien, présent au Plio-Pléistocène en Méditerranée (ZIBROWIUS et HOVE, 1987); *N. sphaeropomatus* de Nouvelle-Zélande (STULL, 1979) et *N. globula* (DEW, 1959) du sud-ouest de l'Australie. *Neovermilia anoperculata* s'en distingue donc par l'absence d'opercule.

Remerciements

Je remercie J. LE LANNIC du Centre Commun de Microscopie Électronique à Balayage de l'Université de Rennes I et Y. GRUET du Laboratoire de Biologie Marine de l'Université de Nantes pour les photos des tubes au MEB.

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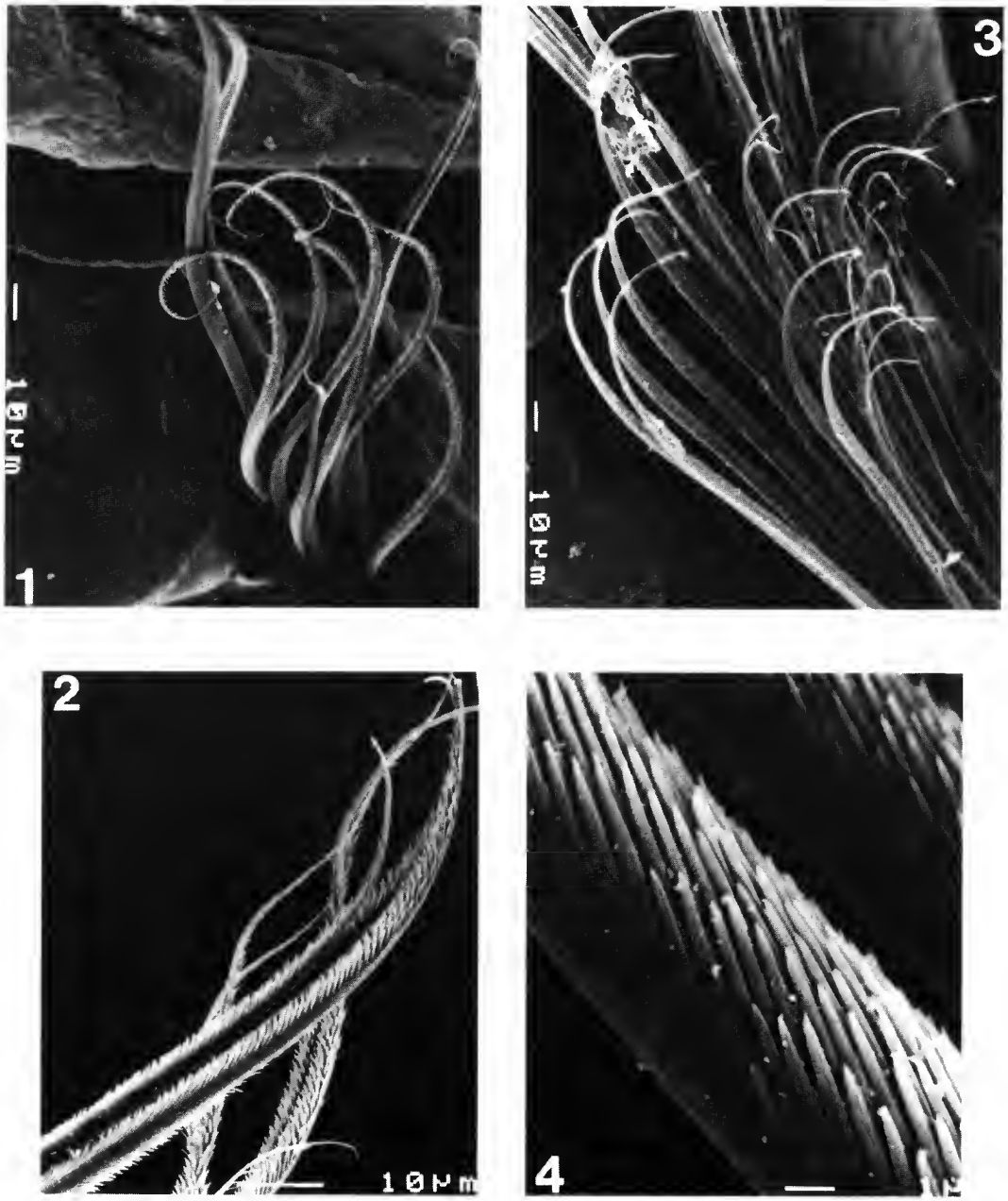
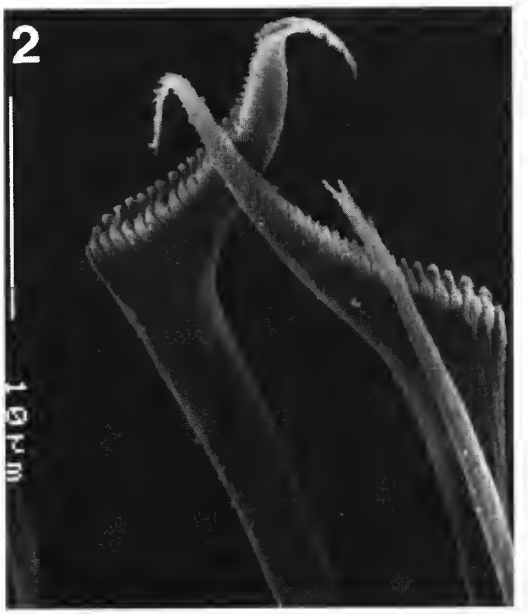
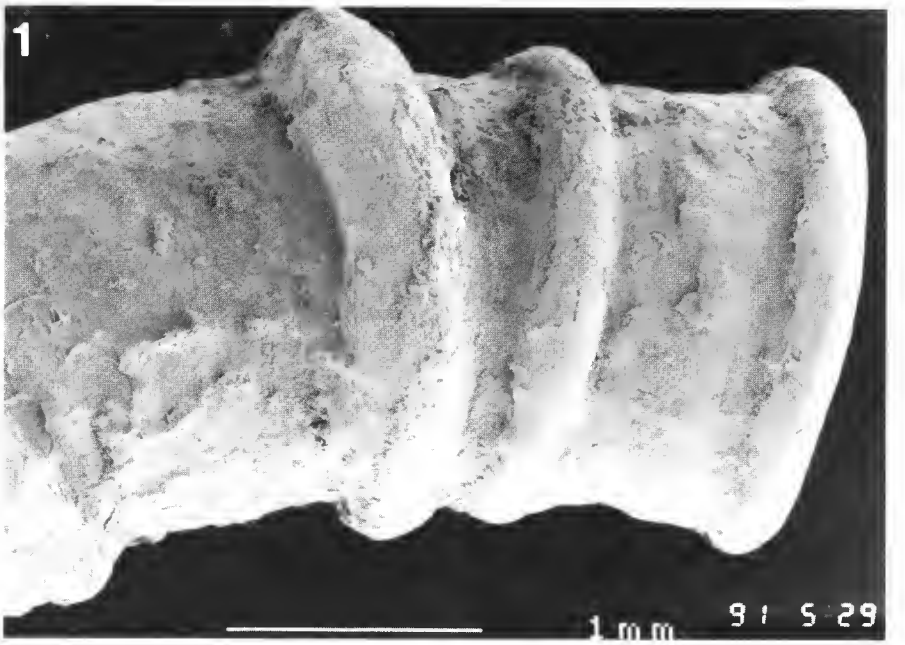
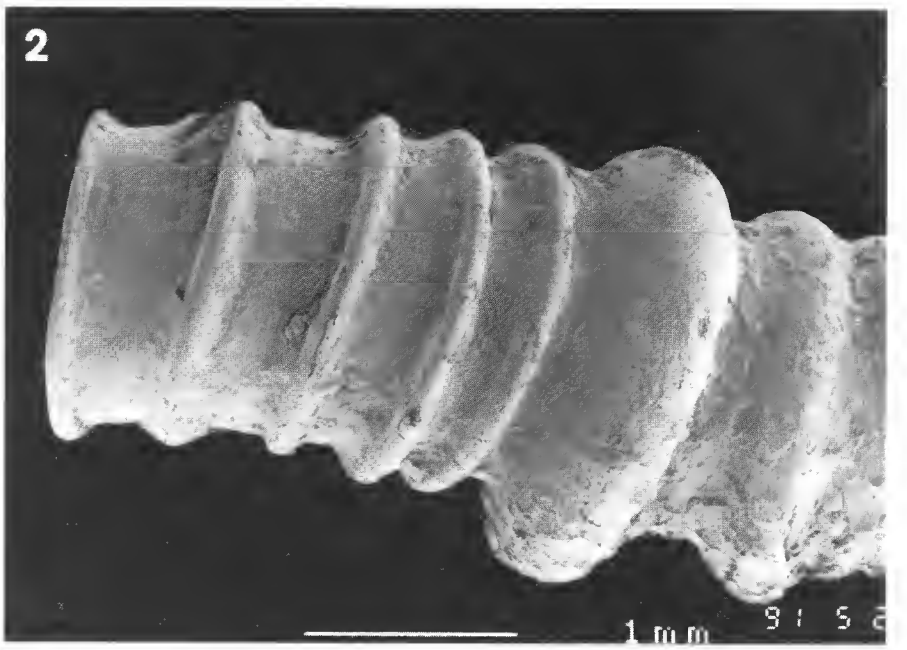


PL. I. — *Neovermilia anoperculata* sp. nov. : 1, soies du premier sétigère; 2, détail des soies du 1er sétigère; 3, soies thoraciques; 4, détail des soies thoraciques.



Pl. II. — *Neovermilia anoperculata* sp. nov. : 1, uncini thoraciques; 2, soies abdominales; 3, uncini abdominaux.





PL. III. — *Neovermilia anoperculata* sp. nov. : 1-2, parties antérieures du tube.

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section A, n° 2 : 449-455.

Neotonchinae de la Baie de Morlaix (Nematoda, Chromadorida)

par Nicole GOURBAULT et Magda VINCX

Résumé. — Six espèces d'Ethmolaimidae ont été identifiées en Manche occidentale (Baie de Morlaix), dont une nouvelle, *Comesa platti* sp. n. Portant à onze le nombre d'espèces de ce genre, cette dernière est caractérisée par la taille très réduite des soies séphaliques, la position antérieure des amphides, l'absence de différenciation latérale et les papilles précloacales au nombre de 9 à 11.

Abstract. — Six species of the family Ethmolaimidae, including the new species *Comesa platti* sp. n., are identified from the Western part of the Channel (Baie de Morlaix). Within the genus *Comesa*, which has eleven species at present, the new species is characterized by its short cephalic setae, the anterior position of the amphids, the absence of lateral differentiation and the presence of 9-11 precloacal supplements.

Key-words — Nématodes marins, *Comesa*, Manche.

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INTRODUCTION

Un suivi écologique des peuplements de nématodes marins de la Baie de Morlaix portant sur plusieurs années (GOURBAULT, 1981, 1987) a permis la récolte de nombreux spécimens de la sous-famille des Neotonchinae. Les espèces identifiées appartiennent aux deux genres *Neotonchus* Cobb, 1933 et *Comesa* Gerlach, 1956, taxons toujours signalés dans la littérature par un très faible nombre d'individus et dont la première révision a été effectuée par WIESER et HOPPER (1966); nous devons les plus récentes à PLATT (1982, et 1985 sur ce même matériel de la Baie de Morlaix).

Deux espèces de *Neotonchus* sont présentes : *N. meeki* Warwick, 1971 et *N. boucheri* Platt, 1982 décrites respectivement de la Mer du Nord (Northumberland) et de la Manche Ouest (Pierre Noire, Morlaix). Les espèces de *Comesa* sont représentées par l'espèce-type, *C. corcunda* Gerlach, 1956 et aussi par *C. interrupta* et *C. votadiini* (Warwick, 1971) encore signalée en Mer du Nord (HEIP, HERMAN & VINCX, 1983).

Mais l'espèce dominante est nouvelle; elle peuple l'ensemble du chenal de la Baie de Morlaix avec toutefois une plus nette abondance aux stations moyennes, plus envasées, alors que la seconde espèce en rang d'abondance, *N. meeki*, s'observe essentiellement dans la partie sableuse, en aval du chenal.

Matériel et méthodes

Récoltes, tris et montages ont été effectués de façon classique et à présent standardisée pour ce groupe (Vincx & Gourbault, 1988). Les spécimens-types ont été déposés dans les collections nationales du Muséum national d'Histoire naturelle (MNHN) et du Zoology Institute, Gent (RUG).

Famille Ethmolaimidae Filipjev et Stekhoven, 1941

Sous-famille Neotonchinae Wieser et Hopper, 1966

Genre **COMESA** Gerlach, 1956

[Syn. *Neotonchoides* Platt, 1982]

Comesa platti sp. n.
(Fig. 1)

Matériel-type : Holotype ♂1, lame BN 143 (MNHN); paratypes BN 144-155 (MNHN) et n° 10262-10263 (RUG).

Localités : Baie de Morlaix, tout au long du chenal, essentiellement en amont (—15 m) mais aussi au large (st. 7, cf. Gourbault, 1981).

Habitat : Marin, dans le sédiment sublittoral fin (50 < Md < 240 μm) et envasé (20 < % pélites < 50).

Étymologie : Espèce amicalement dédiée au Dr. Howard Platt, Department of the Environment, Belfast, Northern Ireland, en reconnaissance de son travail de révision des Ethmolaimidae et en remerciement pour l'intérêt qu'il a porté à ce matériel.

Mesures (longueurs en μm, moyennes et écart-types) :

Holotype ♂1 : $\frac{— \ 90 \ M \ 620}{8 \ \ 19 \ 21 \ 18}$ 680; a = 32,3; b = 7,5; c = 11,3; c′ = 3,3.

Paratypes : mâles (n = 26) : nb papilles précloacales = 10 ± 1; L = 700 ± 40; a = 29,9 ± 2,2; b = 7,9 ± 0,5; c = 11,8 ± 0,9.

Paratype ♂1 : $\frac{— \ 85 \ 330 \ 600}{9 \ \ 19 \ 25 \ 18}$ 665; a = 26,5; b = 7,8; c = 10,2; V = 49,6.

Femelles (n = 31) : V = 49,5 ± 1,4; L = 670 ± 54; a = 25,8 ± 3,2; b = 7,7 ± 0,5; c = 10,2 ± 0,8.

Juvénile : $\frac{— \ 75 \ M \ 500}{8 \ \ 16 \ 16 \ 15}$ 560; a = 35; b = 7,5; c = 9,3.

Description

Mâles

Corps cylindrique avec atténuation plus nette dans la région postérieure que dans la partie antérieure où elle est faible et confère un aspect carré à la tête. Cuticule à rangées transversales resserrées (dix pour 5 µm) de très fines ponctuations arrondies et homogènes, débutant en arrière des soies céphaliques et atteignant l'extrémité caudale ; absence de différenciation latérale (fig. 1A).

Six minuscules papilles labiales internes peu visibles, six soies labiales externes et quatre soies céphaliques papilliformes (1 µm) ; une paire de courtes soies subcéphaliques (1,5 µm) latéro-dorsales situées à 4-5 µm en arrière de l'amphide. Amphide spiralée à 2 1/2 tours, en position assez antérieure, sa partie médiane atteignant le niveau des soies céphaliques, et de 4 µm de largeur, soit 45 % du diamètre correspondant de la tête.

Cavité buccale moyennement développée avec petite dent dorsale pointue et deux paires de denticules ventraux. Pharynx long (90 µm) et cylindrique avec un court bulbe terminal ovoïde (17 × 14 µm) ; cardia développé (9 µm). Anneau nerveux à 55 % de la longueur du pharynx. Glande excrétrice ventrale volumineuse ouvrant par un très petit pore ventral, situé au niveau des soies céphaliques, suivi d'une longue (24 × 4 µm) ampoule très antérieure (fig. 1B). Intestin à longues cellules dans sa partie antérieure.

Queue typique de Neotonchinae, légèrement recourbée ventralement (fig. 1G).

Mâle diorchique à testicules en tandem, antérieur droit, court, épais, débutant à une centaine de µm en arrière de la base du pharynx et placé le plus souvent à la gauche du tube digestif ; testicule postérieur toujours moins développé, réfléchi, ce qui peut donner l'impression que les testicules sont opposés (fig. 1C). Longues vésicules séminales à spermatozoïdes globuleux, très granuleux (10-12 µm). Vas deferens à cellules granuleuses également, mais les granulations sont plus petites et de taille hétérogène en général, à l'exception de deux zones : juste en avant de la première papille précloacale, et aussi avant le « clear patch » au niveau des 3-4e papilles.

Spicules pairs, coudés dans leur tiers postérieur, à pointe effilée et capitulum légèrement évasé, long de 24-25 µm, soit 1,5 fois la longueur du diamètre corporel au niveau de l'anus. Gubernaculum (17-18 µm) en deux lames minces à partie proximale effilée et distale à peine recourbée, s'écartant des spicules en arrière de la courbure. Une soie préanale (3 µm) à une dizaine de µm en avant du pore cloacal précède la série des papilles précloacales situées à égale distance les unes des autres, soit 12 µm, et au nombre de neuf à onze généralement (douze papilles chez deux des mâles). Ces cupules à ouverture circulaire présentent en outre l'étroit bourrelet longitudinal articulé caractéristique du groupe (fig. 1G-H).

Femelles

Elles diffèrent essentiellement des mâles par la morphologie de la queue (c′ = 3,6 au lieu de 3,3).

Didelphes, à ovaires opposés et réfléchis ; vagin entouré d'une forte musculature et accompagné de deux petites glandes sphériques granuleuses. Chambre utérine impaire peu

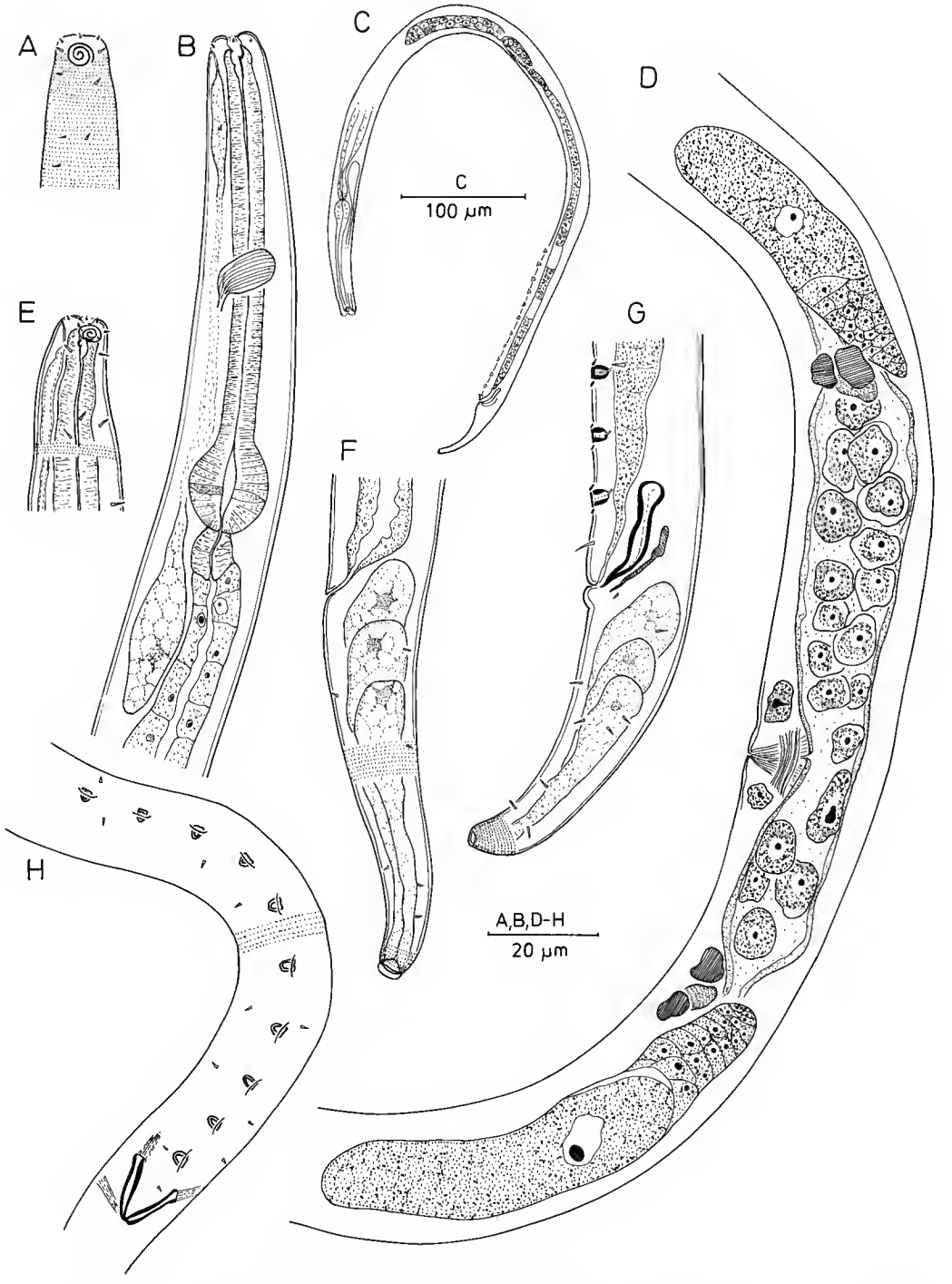

FIG. 1. — *Comesa platti* sp. n. Holotype ♂1 : A, partie antérieure en vue latérale superficielle et B, en coupe optique sagittale, C, habitus. Paratype femelle ♀1 : D, système reproducteur, E, partie antérieure en coupe optique et F, partie postérieure. G, appareil copulateur et queue du ♂1. H, vue ventrale de la partie postérieure d'un paratype mâle au niveau des papilles cloacales.

développée et spermathèques renfermant de gros spermatozoïdes analogues à ceux des vésicules mâles, en nombre relativement réduit du fait de leur grande taille. Présence de corpuscules globuleux réfringents au départ des oviductes (fig. 1D).

Juvéniles à habitus semblable à celui des adultes.

DIAGNOSE DIFFÉRENTIELLE : La nouvelle espèce, *Comesa platti* sp. n., est caractérisée par la taille très réduite des soies céphaliques, la morphologie de l'amphide et le nombre de papilles précloacales ; pas de différenciation latérale de la cuticule. Ces traits la rapprochent essentiellement de *C. interrupta* ; chez cette dernière espèce, les spicules sont légèrement plus longs (27-28 µm) mais de forme nettement différente, le gubernaculum est moins développé, et les papilles précloacales sont plus petites. L'ornementation cuticulaire consiste encore en ponctuations plus espacées chez la nouvelle espèce.

Comesa votadinii (Warwick, 1971)
(Fig. 2)

Neotonchus votadinii Warwick, 1971 : 105-106, fig. 6 (1♂, 1♀).
C. votadinii ; PLATT, 1985 : 148, fig. 9.

MATÉRIEL ÉTUDIÉ : 10♂♂, 2♀♀, 1 juv., lames AN 659-662, 665-667 (MNHN) et n° 10264-10265 (RUG).

LOCALITÉS : Baie de Morlaix, tout au long du chenal.

HABITAT : Marin, dans le sédiment fin à moyen (55 < Md < 650 µm) et envasé (11 < % pélites < 50) du chenal.

MESURES (longueurs en µm) :

Mâles : ♂1 : $\frac{— \ 116 \ M \ 710}{7 \ 28 \ 29 \ 27}$ 790 ; a = 27,2 ; b = 6,8 ; c = 9,9 ; c′ = 3. — (n = 9) : nb : papilles précloacales 14 (13-15) ; L = 765 (650-830) ; a = 27,0 (21-33,2) ; b = 6,9 (6,5-7,6) ; c = 10,4 (9,4-11,8) ; long. spicules = 34 (31-38).

Femelles : ♀1 : $\frac{— \ 104 \ 400 \ 722}{7 \ 29 \ 35 \ 27}$ 790 ; a = 22,5 ; b = 7,6 ; c = 11,6 ; V = 50,6. — ♀2 ; L = 870 ; a = 23,1 ; b = 7,0 ; c = 9,5 ; V = 51,1.

REMARQUES

Cette espèce, décrite sur deux individus et dont quelques exemplaires du chenal ont été confrontés au spécimen-type par PLATT (1985), est bien caractérisée par l'amincissement de l'extrémité antérieure et le rapprochement des deux dernières couronnes de papilles labiales externes et soies céphaliques, mais aussi par la largeur de l'amphide occupant 60 % du diamètre céphalique à ce niveau. La paire de soies subcéphaliques est située en arrière de l'amphide. La ponctuation consiste en points assez gros et espacés (10 rangs pour 10 µm) et comme chez *C. platti*, aucune différenciation latérale n'existe. Le bulbe pharyngien présente également une forme en losange caractéristique.

Le système copulateur est bien identifiable, spicules pairs et arqués à capitulum marqué, gubernaculum en lames (fig. 2D).

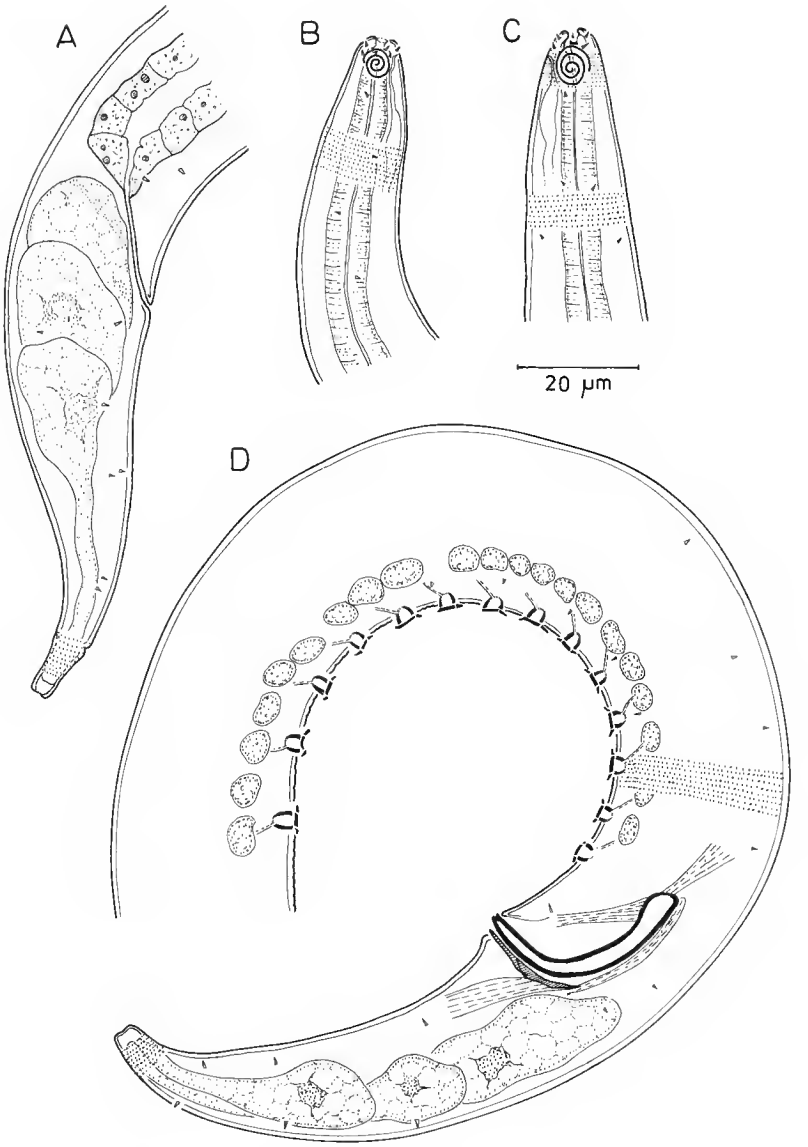

FIG. 2. — *Comesa votadinii* : A, partie postérieure d'une femelle, B-C, partie antérieure, respectivement, de cette même femelle et d'un mâle ; D, partie postérieure du mâle.

En revanche, les femelles sont assez difficiles à différencier de celles de *C. platti*. Cependant, l'amphide est ici proportionnellement plus petite, la queue plus trapue (c' = 2,5 au lieu de 3,6), les spermatozoïdes contenus dans l'utérus sont de taille deux fois moindre (4-5 µm au lieu de 10-12 µm) et il n'existe pas de corpuscules réfringents dans l'oviducte.

Le nouveau taxon porte à onze le nombre d'espèces de *Comesa* décrites à ce jour : *C. corcunda* Gerlach, 1956, *C. cuanensis* (Platt, 1982), *C. cupulata* (Vitiello, 1970), *C. interrupta* (Warwick, 1971), *C. melotrida* (Wieser et Hopper, 1966), *C. platti* sp. n., *C. pseudocorcunda* (Vitiello, 1971), *C. vitia* (Warwick, 1971), *C. vitielloi* (Platt, 1982), *C. votadinii* (Warwick, 1971) et *C. warwicki* (Platt, 1982).

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Un genre oublié d'Atractosomatinae des Alpes italo-suisses, *Bomogona* Cook, 1895 : statut, contenu, chorologie (Diplopoda, Craspedosomatida)

par Ariane PEDROLI-CHRISTEN et Jean-Paul MAURIÈS

Résumé. — La redécouverte fortuite des échantillons-types d'*Atractosoma lombardicum* Brölemann, 1892, espèce-type du genre oublié *Bomogona* Cook, 1895, au Muséum national d'Histoire naturelle de Paris, permet une mise à jour nomenclaturale qui vient à point nommé compléter une révision systématique et chorologique s'appuyant sur d'abondantes récoltes effectuées récemment dans le Valais et le Tessin. Des taxons traditionnellement et confusément considérés comme appartenant aux genres ou sous-genres *Atractosoma* Fanzago, 1886, *Ceratosoma* Verhoeff, 1897, *Triakontazona* Verhoeff, 1897, *Limnalpium* Verhoeff, 1921, *Asandalum* Attems, 1949 et plus récemment aux genres *Ochogona* Cook, 1895 et *Ornithogona* Cook, 1896, géographiquement cantonnés au sud de la Suisse et au nord-ouest de l'Italie, appartiennent en fait à un seul genre, *Bomogona* Cook, 1895, et à deux espèces : *Bomogona lombardica* (Brölemann, 1892) [syn. nov. : *Ceratosoma luganensis* et *luganensis ruscorum* Verhoeff, 1921, *Ceratosoma fontis* Verhoeff, 1932]; *Bomogona* (*Ornithogona*) *helvetica* (Verhoeff, 1894) [syn. nov. : *Atractosoma helveticum dentatum* Faës, 1902, *Ceratosoma verbani* Verhoeff, 1910, et *Dorasoma quercuum* Verhoeff, 1932].

Abstract. — The revision of the type of *Atractosoma lombardicum*, type-species of the forgotten genus *Bomogona* Cook, 1895, in collection at the Muséum national d'Histoire naturelle of Paris, and the analysis of abundant material recently collected in Switzerland, allowed a nomenclatorial, systematic and chorological revision of the taxa successively and confusedly called *Atractosoma* Fanzago, 1886, *Ceratosoma* Verhoeff, 1897, *Triakontazona* Verhoeff, 1897, *Limnalpium* Verhoeff, 1921, *Asandalum* Attems, 1949, *Ochogona* Cook, 1895 and *Ornithogona* Cook, 1896. These are revised to a single genus, *Bomogona* Cook, 1895, and two species : *Bomogona lombardica* (Brölemann, 1892) [syn. nov. : *Ceratosoma luganensis* et *luganensis ruscorum* Verhoeff, 1921, *Ceratosoma fontis* Verhoeff, 1932]; *Bomogona* (*Ornithogona*) *helvetica* (Verhoeff,1894) [syn. nov. : *Atractosoma helveticum dentatum* Faës, 1902, *Ceratosoma verbani* Verhoeff, 1910, and *Dorasoma quercuum* Verhoeff, 1932]. These species are distributed in the southern part of Switzerland and in the north-west of Italy.

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INTRODUCTION

Les nombreux articles qui traitent de certaines espèces de Diplopodes Craspedosomides de Suisse et du nord de l'Italie autrefois classées dans les genres *Euceratosoma* Verhoeff, 1897 (alias *Ceratosoma* Verhoeff, 1897) ou *Atractosoma*, et plus récemment dans les genres *Ornithogona* Cook, 1896, *Ochogona* Cook, 1895, *Triakontazona* Verhoeff, 1897, *Limnalpium*

Verhoeff, 1921, *Dorasoma* Verhoeff, 1932 et *Asandalum* Attems, 1949 font ressortir une certaine confusion et des contradictions qui rendent nécessaire une clarification des problèmes nomenclaturaux et taxonomiques afférant à ces taxons.

C'est pourquoi nous avons procédé, d'une part, à une approche historique des données et, d'autre part, à la comparaison des récoltes effectuées par l'un de nous (A. P.) avec les matériels types.

Dans le cadre volontairement limité de cette note, ne seront considérés ici que des Atractosomatinae ayant été classés dans les taxons de rang générique énumérés ci-dessus. Nous verrons plus loin qu'ils appartiennent en fait à un seul genre, géographiquement localisé à l'ensemble formé par le Valais, le Tessin, l'Aoste, le Piémont et la Lombardie (avec une pointe avancée méridionale vers le Nord-Appenin).

Matériel et méthodes

L'un de nous (A. P.), au cours de ces dernières années, a récolté personnellement ou rassemblé pour identification (dans le cadre d'études pluridisciplinaires), en Suisse, et plus particulièrement dans le Valais et le Tessin, par chasse à vue et par piégeage (Barber), 240 exemplaires adultes d'Atractosomatinae se rattachant aux taxons évoqués ci-dessus. Cet important matériel, récolté dans 20 stations pour la plupart inédites, a été comparé, pour identification, avec les figures et descriptions des auteurs, mais aussi avec les matériels des collections ci-après :

— **Collection Verhoeff, de la Staatssammlung de Munich** : *Ceratosoma luganensis* Verhoeff, 1921 : 1 mâle, 1 femelle de Borgotaro, 1 mâle de Torre Pellice, 1 mâle de Toron (Como), 1 femelle de Campo di Fiori (Varese), 2 mâles de Ceres ; *Ceratosoma luganensis ruscorum* Verhoeff, 1921 : 1 mâle, 2 femelles de Como ; *Ceratosoma verbani* Verhoeff, 1910 : 1 mâle, 1 femelle de Bellinzona ; *Dorasoma helveticum* (Verhoeff, 1894) : 16 mâles, 6 femelles de Stalden (850 et 900 m) et 1 mâle, 9 femelles de Zermatt (1750 m) ; *Dorasoma serratum* Verhoeff, 1932 : 1 mâle, 2 femelles d'Aoste ; *Dorasoma quercuum* Verhoeff, 1932 : 1 mâle d'Ivrea ; *Ceratosoma larii* Verhoeff, 1921 : 1 mâle, 3 femelles de Bellano.

— **Collection du Muséum national d'Histoire naturelle de Paris** : Les échantillons originaux ayant servi à la description de *Atractosoma lombardicum* Brölemann, 1892 ont été retrouvés à la faveur de rangements entrepris récemment. Des 10 individus (6 mâles et 4 femelles) cités par l'auteur de la localité originale (environs de Varese), n'ont été retrouvés que 4 mâles, 3 exemplaires sans partie antérieure et une femelle préadulte. Du matériel cité par Brölemann dans sa deuxième note sur la Lombardie en 1895, ont pu être examinés : 3 exemplaires dont 1 mâle de Erba (Como), 11 jeunes de Lecco (Como), 1 femelle du Monte Resegone (Como), 1 femelle du Val Ganna (Varese).

— **Collection Faës du Muséum d'Histoire naturelle de Lausanne** : *Atractosoma helveticum dentatum*, représenté par un mâle disséqué aux gonopodes malheureusement perdus.

— **Autres matériels** : Quelques échantillons étudiés par l'un de nous (J.-P. M.), appartenant à des localités inédites, figurent dans ce travail ; ils proviennent, soit d'inédits provenant des collections du Muséum national d'Histoire naturelle de Paris, soit de récoltes effectuées par Desmond Kime (Bruxelles) ou rassemblées par Marco Valle (Musée de Bergamo).

I. Historique

Brölemann (1892 : 108, fig. 6) décrit *Atractosoma lombardicum* sur 6 mâles et 4 femelles récoltés en deux localités des environs de Varese (Vedano-Olona et Gavirate). Cette espèce,

bien que citée une deuxième fois par BRÖLEMANN (1895), qui donne de nouvelles localités lombardes (Val Ganna, Erbe, Lecco, Monte Resegone, Comune) va rester, probablement en raison de l'insuffisante clarté des dessins des gonopodes, complètement ignorée de la quasi-totalité des auteurs.

Ainsi, VERHOEFF (1894) n'y fait aucune allusion et ne la compare pas à son *Atractosoma helveticum* (p. 286, fig. 1-3), décrit sur un mâle récolté à Zermatt.

Par contre, COOK (1895 : 2) estime sans doute la description de l'espèce de BRÖLEMANN suffisante puisqu'il la désigne, certainement sans en avoir vu un seul échantillon, comme type d'un nouveau genre *Bomogona*. Création qu'il effectue en même temps que plusieurs autres (dont *Ochogona* pour *Atractosoma pusillum* Verhoeff, 1893), sur la base des seules descriptions d'espèces qui en l'occurrence tiennent lieu de diagnose. De la même façon il crée, un peu plus tard (COOK, 1896 : 8), *Ornithogona*, pour *Atractosoma helveticum* Verhoeff, 1894.

De son côté, VERHOEFF (1897 : 131), ignorant les travaux de son collègue américain, dont on sait que la diffusion a été très confidentielle, inclut cette dernière espèce, dont il est l'inventeur, dans un nouveau genre *Triakontazona* (dans lequel il classe aussi *pusillum*). Dans le même travail, à la même page, il crée un autre genre, *Ceratosoma* (type *apfelbecki* n. sp.) qui englobera plus tard (VERHOEFF, 1899 : 140-141) *Triakontazona* relégué au rang de sous-genre [1].

FAËS (1902 : 83, fig. 27-30), probablement non informé de ces péripéties, continue à utiliser le nom de genre *Atractosoma* et décrit du Valais (Ardon et Mauvoisin) une nouvelle forme, *dentatum*, qu'il considère comme sous-espèce de *A. helveticum* et qui se distingue, selon lui, par la présence, à l'apex des syncoxites des gonopodes, d'une structure en lamelle denticulée non signalée dans la description du type par VERHOEFF, (1894).

VERHOEFF (1910 : 314, fig. 124-127) décrit sur un seul mâle, de Laveno (Lac Majeur), *Ceratosoma* (*Triakontazona*) *verbani* qui ressemble beaucoup à *helveticum* tant par sa morphologie externe que par sa structure gonopodiale ; il signale de petites différences aux cheirites et aux syncoxites.

VERHOEFF (1921 : 27-29, fig. 20-26) décrit trois taxons dont l'un est pratiquement sympatrique de l'espèce de BRÖLEMANN : *Ceratosoma larii*, récoltée à Bellano et à Rovinato, près de Lecco (lac de Come), ne sera jamais plus citée dans la littérature hormis dans des listes (ATTEMS, 1949 ; STRASSER et MINELLI, 1984) ; *Ceratosoma luganensis*, récoltée en Suisse à Melide, près de Lugano (Tessin), avec une sous-espèce *C. l. ruscorum*, récoltée en territoire italien à Como, sera par contre retrouvée et citée plusieurs fois par la suite.

Dans la même note, VERHOEFF classe ces taxons, avec *C. helveticum* (incluant son nouveau syn. *dentatum* Faës) et *C. verbani*, dans un nouveau sous-genre de *Ceratosoma* : *Limnalpiun*. Il apporte quelques précisions sur la structure gonopodiale de *C. verbani* (fig. 27) dont il a récolté cinq mâles et cinq femelles à Bellinzona (Tessin) : il signale au coxosternite des paragonopodes des prolongements paramédians qui sont absents chez *C. helveticum*.

ATTEMS (1927 : 105), à l'occasion de la description de deux espèces d'Autriche et de Yougoslavie, valide le sous-genre *Limnalpium* Verhoeff, 1921 en désignant comme espèce-type : *A. helveticum* ; il lui conserve le même contenu que VERHOEFF (1921) : *verbani, helveticum, larii, luganense*.

VERHOEFF (1932 : 604-606, fig. 15-20) crée un nouveau genre *Dorasoma* pour deux espèces

1. Pour remplacer *Ceratosoma*, nom deux fois préoccupé, ont été proposés d'une part *Ceratosomana* Strand, 1928 et d'autre part *Euceratosoma* Verhoeff, 1897 (validé par JEEKEL, 1971).

nouvelles récoltées en Val d'Aoste : *D. serratum* (Aoste) et *D. quercuum* (Ivrea, près du Lac Sirio). Pour son inventeur, ce genre se distingue de *Limnalpium*, dont il est très proche, par la présence d'une lame dentée sur les syncoxites des gonopodes. Dans ce même travail, il décrit (p. 607, fig. 21-23) une nouvelle espèce récoltée à Torre Pellice (Piémont) : *C.* (*Limnalpium*) *fontis*.

VERHOEFF (1936*a* : 206-207), s'appuyant sur de nouvelles récoltes effectuées dans le Haut-Valais (p. 214 : Zermatt, vallée de Saas à Stalden, Visp), décèle pour la première fois chez *C.* (*L.*) *helveticum* la lame dentée des syncoxites gonopodiaux déjà décrite et figurée par FAËS (1902) pour sa forme *dentatum* : il considère ce caractère comme très important et caractéristique du genre *Dorasoma* qu'il avait créé en 1932 pour les deux « espèces » *quercuum* et *serratum*, auxquelles il ajoute *helveticum*.

VERHOEFF (1936*b* : 404), à la faveur de nouvelles récoltes effectuées au Piémont (Felsen près Ceres, Ala di Stura, Pinerolo, Barge) et dans le Nord-Appenin (Borgotaro), s'aperçoit que son *C.* (*L.*) *fontis* est en fait synonyme de *C.* (*L.*) *luganensis* Verhoeff, 1921.

Dans la liste des taxons est-alpins donnée par ATTEMS (1949 : 137)), apparaît un nouveau nom de genre, *Asandalum*, créé probablement avec l'intention louable (mais inutile puisqu'il existait *Euceratosoma* Verhoeff, 1899) de remplacer *Ceratosoma* (nom deux fois préoccupé !). Parmi les 27 taxons regroupés par ATTEMS sous ce nom de genre, nous retrouvons *luganensis, verbani, quercuum* et *larii*.

STRASSER (1978 : 151) signale dans la plaine du Piémont *Dorasoma helveticum* (Verh., 1894) pr. *quercuum* Verh., 1932 (Castelleto Ticino); pour lui, *D. serratum* et *D. quercuum* ne sont pas des espèces. Il signale également dans la même région (Lombardore), mais aussi dans les Alpes Graies (Torre del Colle), la présence de *Triakontazona* (*Limnalpium*) *luganense* Verhoeff, 1921.

HOFFMAN (1979 : 125) trouve injustifié le long oubli dans lequel est restée l'espèce-type de *Bomogona, Atractosoma lombardicum*, et précise qu'il ne peut, avant toute révision, se prononcer clairement sur la place de *Bomogona* parmi les autres taxons de rang générique de la sous-famille des Atractosominae.

Ceci explique pourquoi dans la liste des Diplopodes d'Italie de STRASSER et MINELLI (1984) où sont adoptées, au niveau des genres, les options nomenclaturales proposées par HOFFMAN (1979), *Bomogona lombardicum* n'apparaît pas. Les autres taxons qui nous intéressent ici sont classés, l'un (*helvetica*) dans le genre *Ornithogona*, les autres (*verbani, luganensis* et *larii*) dans le genre *Ochogona*.

KURNIK (1896) décrit les caractères de la femelle d'*Ochogona luganensis* sur du matériel provenant de la collection VERHOEFF (Staatssamml. München); il s'agit de spécimens signalés par VERHOEFF (1936) du Nord-Apennin (Borgotaro) sous le nom de *Ceratosoma* (*Limnalpium*) *luganensis*.

La seule revue de cette bibliographie, avant même tout examen de matériel, permet de dresser (ci-après) une liste provisoire de cinq groupes de citations et/ou mentions de taxons manifestement synonymes. Ceux qui ne sont que des combinaisons de noms sont indiqués par un astérisque.

1 — *Atractosoma lombardicum* Brölemann, 1892
Atractosoma lombardicum Brölemann, 1895
**Bomogona lombardica* Cook, 1895
**Bomogona lombardicum* Hoffman, 1979

2 — *Atractosoma helveticum* Verhoeff, 1894
**Ornithogona helvetica* Cook, 1895
**Triakontazona helvetica* Verhoeff, 1897
Atractosoma helveticum dentatum Faës, 1902
**Ceratosoma* (*Limnalpium*) *helveticum* Verhoeff, 1921
**Ceratosoma* (*Limnalpium*) *helveticum* Attems, 1927
Dorasoma quercuum Verhoeff, 1932
Dorasoma serratum Verhoeff, 1936
Dorasoma helveticum Verhoeff, 1936
**Asandalum quercuum* Attems, 1949
Dorasoma helveticum quercuum Strasser, 1978
**Ornithogona helvetica* Strasser et Minelli, 1984

3 — *Ceratosoma* (*Triakontazona*) *verbani* Verhoeff, 1910
Ceratosoma (*Limnalpium*) *verbani* Verhoeff, 1921
Ceratosoma (*Limnalpium*) *verbani* Attems, 1927
**Asandalum verbani* Attems, 1949
**Ochogona verbani* Strasser et Minelli, 1984

4 — *Ceratosoma* (*Limnalpium*) *larii* Verhoeff, 1921
Ceratosoma (*Limnalpium*) *larii* Attems, 1927
**Asandalum larii* Attems, 1949
**Ochogona larii* Strasser et Minelli, 1984

5 — *Ceratosoma* (*Limnalpium*) *luganensis* Verhoeff, 1921
Ceratosoma (*Limnalpium*) *luganensis ruscorum* Verhoeff, 1921
Ceratosoma (*Limnalpium*) *luganensis* Attems, 1927
Ceratosoma (*Limnalpium*) *fontis* Verhoeff, 1932
**Asandalum luganense luganense* Attems, 1949
**Asandalum luganense ruscorum* Attems, 1949
**Triakontazona* (*Limnalpium*) *luganense* Strasser, 1978
**Ochogona luganensis* Strasser et Minelli, 1984
?**Ochogona luganensis* Kurnik, 1986

Du seul point de vue nomenclatural, l'affiliation générique des groupes de taxons 1 et 2 ne pose aucun problème puisque chacun des deux contient une espèce-type de genre : *Bomogona* pour le premier, *Ornithogona* pour le deuxième. Le groupe 3 ne contient qu'une seule espèce, manifestement voisine sinon synonyme d'*Ornithogona helvetica*, qu'il est donc logique de classer, comme ne l'ont pas fait les auteurs récents, dans le même genre que le groupe 2, c'est-à-dire *Ornithogona*. La place des groupes 4 et 5 est moins évidente : *larii* et *luganensis*, si l'on en juge par les figures de VERHOEFF (1921), semblent distinctes; elles sont cependant manifestement proches l'une de l'autre et les auteurs récents ont donc eu raison de les considérer comme congénériques; mais c'est une étude systématique telle que celle que nous avons menée, et dont les résultats sont exposés plus loin, qui pouvait seule nous dire si le choix qu'ils ont fait d'*Ochogona* était le bon. Cette étude nous éclairera aussi sur les synonymies que l'on pouvait supposer entre : *larii* et *luganensis* (p. 465); *helvetica* et *verbani* (p. 462); *lombardica* et *luganensis* (p. 462); *Bomogona* et *Ornithogona* (p. 467).

II. Morphologie comparée des gonopodes

1. Taxons *helvetica, verbani, quercuum* et *serratum*

91 mâles se rattachant à ce groupe de taxons (nos groupes 2 et 3), en provenance de 23 localités situées dans le Valais et le Tessin, ont été récoltés ces dernières années. Tous ont une structure des gonopodes semblable ; les syncoxites (S) des gonopodes antérieurs présentent toujours la lamelle dentée caractéristique, signalée pour la première fois par Faës, qui pour elle créa sa « forme » *dentatum*, et pour laquelle Verhoeff créera plus tard son genre *Dorasoma*. Tous ces exemplaires de Suisse présentent également des prolongements paramédians (P) sur le coxosternum des paragonopodes.

Parmi ces spécimens, ceux provenant du Tessin ont été comparés aux mâles (deux préparations) de *verbani*, que Verhoeff avait récoltés à Bellinzona. Rien ne permet de les distinguer les uns des autres. En effet sur les préparations de Verhoeff, les syncoxites (S) des gonopodes présentent sans aucun doute possible la lame dentée signalée plus haut et que, curieusement, Verhoeff n'avait pas observée ni décrite, comme elle lui avait échappé lorsqu'il avait décrit *helvetica* en 1894.

Les autres différences signalées par Verhoeff (1910 et 1921) entre *helvetica* et *verbani* se situent, pour les gonopodes antérieurs, au niveau des dents terminales du cheirite (C) : elles sont plus ou moins écartées et plus ou moins larges ; au niveau des paragonopodes, il y a présence ou absence de prolongements paramédians sur le coxosternum. L'examen des 91 mâles montre que ces différences observées aux cheirites et aux prolongements médians du gonopode sont le fait de variations individuelles qui sont très importantes — elles ne sont dues qu'en partie à l'orientation des objets sur lame microscopique — et englobent donc les « caractéristiques » de *verbani*. Quant aux prolongements paramédians des paragonopodes, il s'agit de formations membraneuses paires ou impaires, plus ou moins transparentes et qui pourraient être invaginables comme des sacs coxaux.

Pour les mêmes raisons, une analyse comparée attentive des préparations de Verhoeff de *serratum, quercuum* et *helveticum* ne permet pas non plus de distinguer ces trois taxons.

La synonymie est évidente entre nos groupes de taxons 2 et 3, qui appartiennent tous à l'espèce « *Atractosoma* » *helveticum* Verhoeff, 1894.

Nous avons figuré ici (fig. 1-6) les pièces gonopodiales d'un mâle de Melera (Val Morobbio) pour montrer, en ce qui concerne les gonopodes antérieurs, l'importance de l'orientation tant au niveau du cheirite (C, fig. 1, fig. 2 à 5), que du syncoxite (S, fig. 1) ; sur ce dernier on voit que, selon l'orientation des deux moitiés, on peut observer ou non les denticulations et comprendre pourquoi elles avaient à un moment échappé à Verhoeff.

2. Taxons *lombardicum* et *luganensis*

Révision d'*Atractosoma lombardicum* Brölemann, 1892.

Localité-type : Italie, Lombardie, Varese, Vedano-Olona et Gavirata, octobre 1887, coll. H. W. Brölemann, 1 mâle lectotype (désigné ici), 3 mâles, 1 femelle préadulte, 3 exemplaires paralectotypes (coll. Myriapodes du MNHN, Paris, n° DA 080).

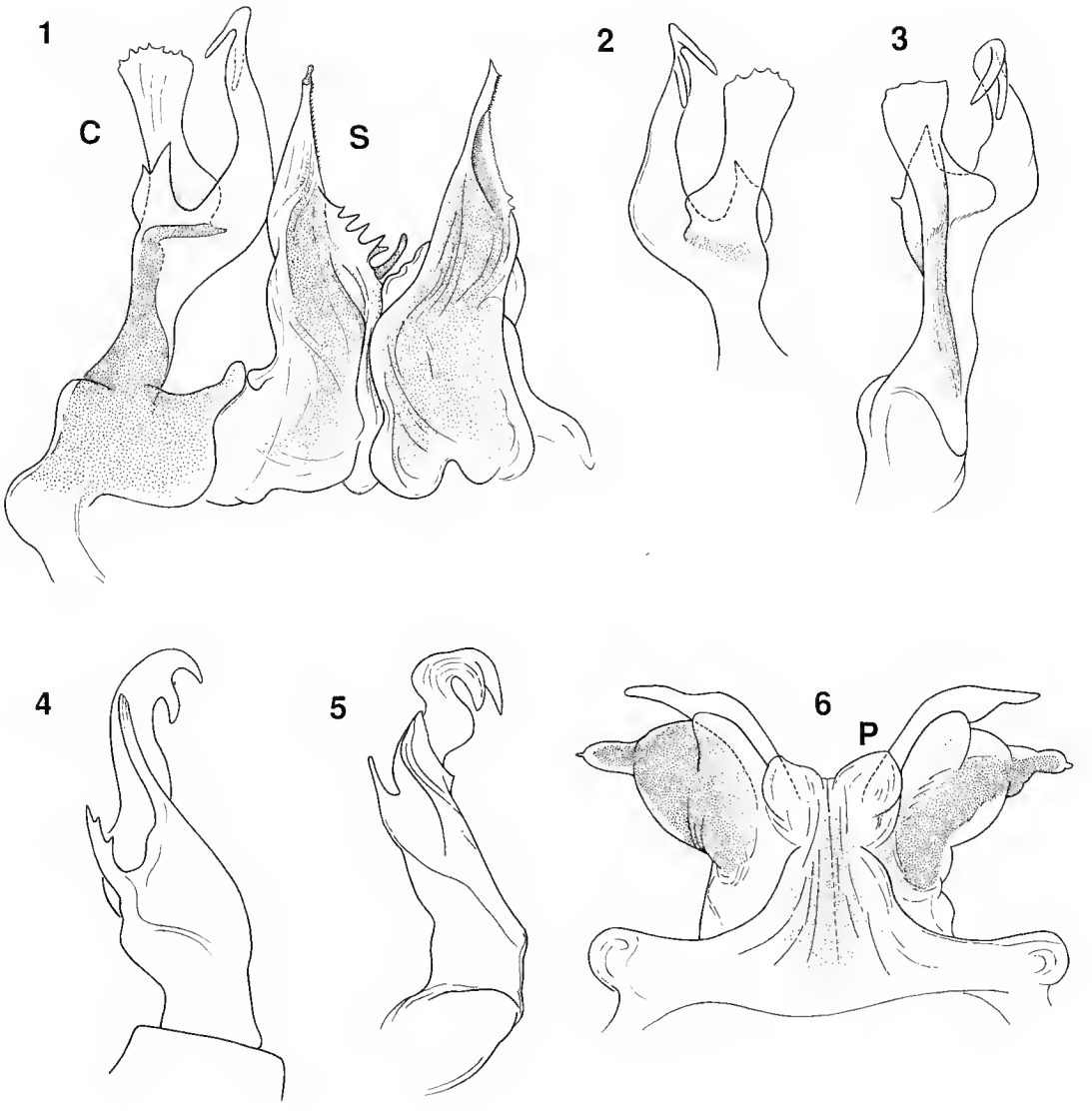

FIG. 1-6. — *Bomogona* (*Ornithogona*) *helvetica* Verhoeff, 1894, mâle de Melera : 1, gonopodes (P.8) en vue caudale de biais montrant le syncoxite (S) et le cheirite (C) droit; 2, cheirite droit en vue externe orale; 3, cheirite gauche en vue orale; 4, le même en vue externe; 5, le même en vue externe distale; 6, paragonopodes (P.9).

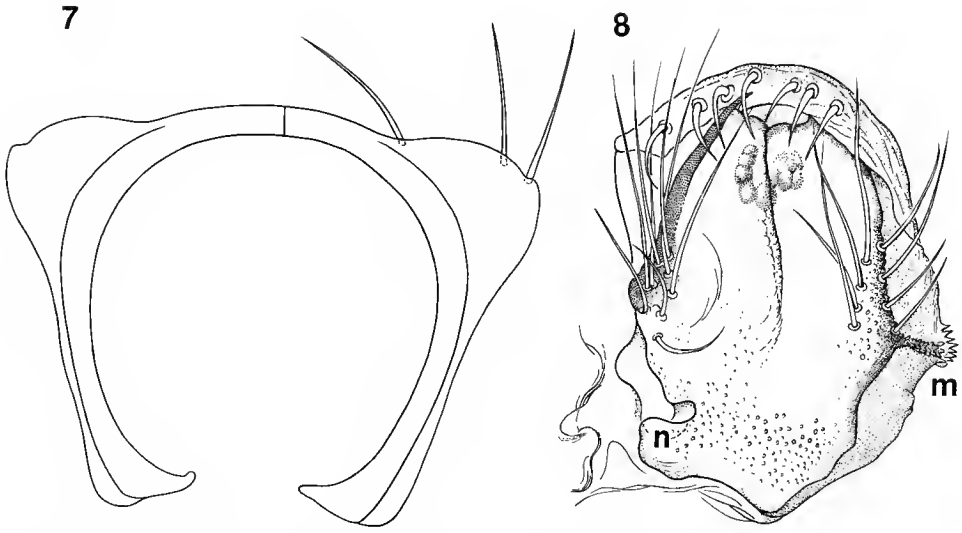

FIG. 7-8. — *Bomogona* (*Ornithogona*) *helvetica* Verhoeff, 1894, femelle de Melera : 7, vue orale d'un anneau moyen ; 8, vulve gauche en vue distale.

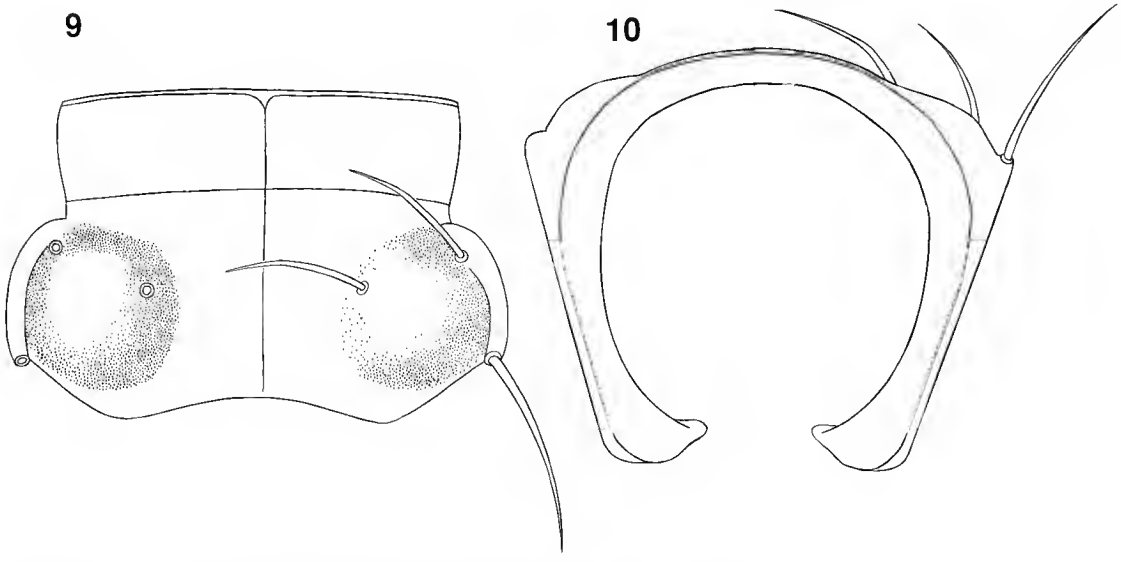

FIG. 9-10. — *Bomogona lombardica* Brölemann, 1892, mâle lectotype : 9, anneau moyen en vue dorsale ; 10, le même en vue orale.

Localités citées par Brölemann (1895) (matériel retrouvé au MNHN, Paris) : Italie, Lombardie, Como : Monte Resegone (près Lecco), 14.08.1892, coll. H. W. Brölemann : 1 femelle jeune à 28 anneaux); Lecco, 31.07.1892, coll. H. W. B. : 1 mâle jeune, 10 jeunes; Erba, 29.08.1891, coll. H. W. B. : 1 mâle, 1 mâle j., 1 exemplaire. — Italie, Lombardie, Varese : Val Ganna, 8.02.1888, coll. H. W. B. : 1 femelle j.

Localité citée par Brölemann (1892) (matériel non retrouvé) : Italie, Lombardie, Varese : Comune.

La description originale des caractères externes est suffisamment précise pour qu'il soit inutile d'y revenir ici. Cependant, pour les paranota des anneaux moyens, dont le texte et la figure 6a de Brölemann (1892) ne donnent qu'une idée imparfaite, il nous a paru nécessaire de donner de nouvelles figurations (fig. 9 et 10) qui permettent de mieux évaluer les distances relatives qui séparent les macrochètes les uns des autres.

Les gonopodes (fig. 11-18) et notamment la silhouette des cheirites (C, fig. 11 et fig. 14-17), vus et dessinés sous différents angles, permettent d'établir sans ambiguité la conspécificité de *lombardicum* et du *luganensis* dessiné par Verhoeff (1921), ce qui ne pouvait se faire au vu des dessins de Brölemann (1892), non seulement parce que ces dessins sont petits et imprécis, mais aussi parce que l'angle sous lequel Brölemann avait dessiné les cheirites ne pouvait que dérouter les comparaisons.

Discussion

Il est manifeste que le matériel récolté ces dernières années et jusqu'à ce jour identifié par nous comme *luganensis*, identification s'appuyant sur les travaux de Verhoeff mais aussi sur le matériel de sa collection, doit, maintenant que *lombardica* est connu, être rapporté à cette espèce. D'autre part, il faut noter que dans les préparations microscopiques définitives telles que celles montées par Verhoeff, il est impossible d'avoir une idée de la tridimensionalité des pièces gonopodiales, ce qui a entraîné des erreurs d'interprétation de la part de Verhoeff lui-même; c'est le cas pour *Ceratosoma* (*L.*) *fontis* que Verhoeff décrivit en 1932 et qu'il mit en synonymie avec *luganensis* quatre ans plus tard, en 1936. La création de *ruscorum* en 1921 ressort probablement d'une semblable méprise, mais aussi peut-être d'une conception différente de celle que nous avons aujourd'hui des limites des variations intraspécifiques.

En conséquence de ce qui précède, il faut regrouper dans la même synonymie les taxons énumérés dans nos groupes 1 et 5; tous appartiennent à l'espèce « *Atractosoma* » *lombardica*.

3. Taxons *larii* et *luganensis*

L'examen de l'unique préparation de *larii* du seul mâle conservé dans les collections de Munich, que nous avons eu sous les yeux, ne nous en apprend malheureusement pas plus que l'examen des figures publiées par Verhoeff (1921). S'il est manifeste que *larii* est plus proche de *lombardica* que de *helvetica*, nous sommes dans l'incapacité de décider aujourd'hui si *larii* est une espèce valide ou une sous-espèce de *lombardica*, ou représente seulement des morphotypes un peu dérivés du fait de leur position externe dans l'aire de cette espèce (voir fig. 19). Nous lui laissons provisoirement le statut de sous-espèce de *lombardica*, et notre groupe 4, qu'elle constituait, doit donc se retrouver avec les groupes 1 et 5.

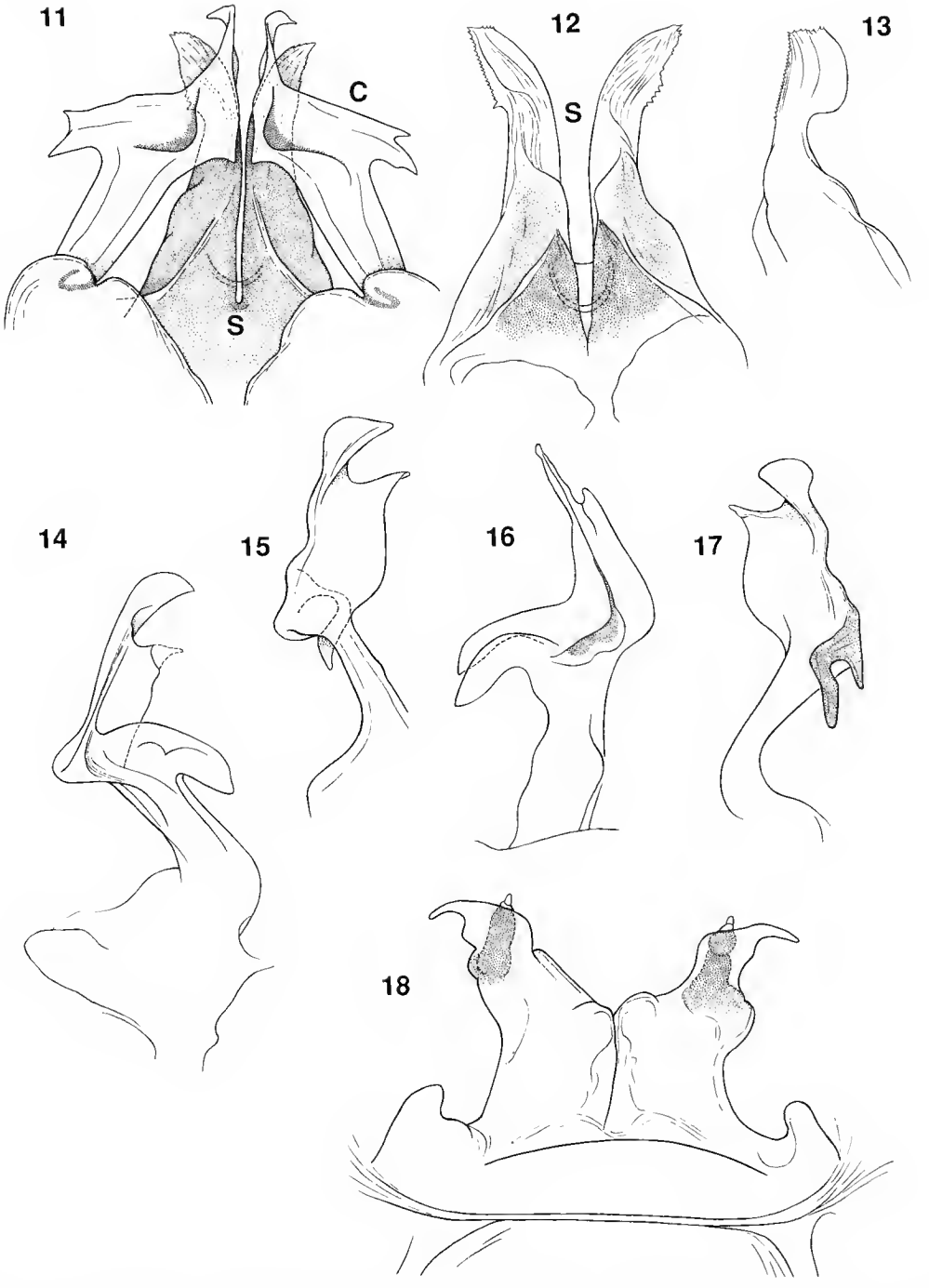

FIG. 11-18. — *Bomogona lombardica* Brölemann, 1892, mâle lectotype : 11, syncoxite (S) et cheirite (C) des gonopodes (P.8) en vue caudale; 12, syncoxite isolé en vue caudale; 13, partie distale d'un coxite, vue latérale; 14, le cheirite gauche en vue caudale externe; 15 à 17, le cheirite droit vu sous différents angles; 18, paragonopodes (P.9).

III. Morphologie comparée des vulves

La seule femelle retrouvée dans le matériel original de *lombardica* n'est pas adulte (28 anneaux) et a été récoltée dans une station qui se trouve sur le territoire de *larii* (à l'est du lac de Côme); il faut certainement la rapporter à ce taxon.

Pour connaître les caractères vulvaires de cette espèce, il faut se reporter aux photos et dessins de vulves donnés par Kurnik (1986), qui ont été réalisés sur les échantillons du Nord-Appenin identifiés comme *luganensis* par Verhoeff (1936). La femelle que nous avons examinée provient du Tessin (Stabio); ses vulves ne se distinguent pas fondamentalement de celles dessinées par Kurnik ; seul, le mamelon spinigère externe paraît ici plus postérieur, peut-être parce que l'angle d'observation est différent.

Quant aux vulves de *helvetica*, elles n'étaient pas encore connues. La figure 8 représente la vulve gauche d'une femelle récoltée à Melera (Val Morobbio); les ressemblances avec les vulves de *lombardica* sont évidentes, y compris par la position du mamelon spinigère (m), et elle ne se distingue que par la présence d'un lobe caudal interne (n) nettement individualisé dans la partie caudale de la valve interne.

IV. Synonymies

Des paragraphes qui précèdent, il s'ensuit que nous nous trouvons en définitive en présence de seulement deux taxons de rang spécifique, l'un *Bomogona lombardica* représenté par nos groupes de synonymes 1, 4 et 5, l'autre, *Ornithogona helvetica* par nos groupes 2 et 3. Chacun de ces taxons est type d'un nom de genre. Cependant, si ces deux espèces sont bien caractérisées morphologiquement l'une par rapport à l'autre, il ne nous semble pas justifié de les considérer comme appartenant à deux genres distincts. Néanmoins, compte tenu des « distances » qui séparent les différents genres d'Atractosomatinae, nous considérons ici *Ornithogona* Cook, 1896, comme sous-genre de *Bomogona* Cook, 1895, et nous proposons donc ici, en attendant la révision d'autres taxons très proches (tels les *Oroposoma* Verhoeff, 1936), la liste synonymique suivante :

Bomogona Cook, 1895

Espèce-type : *Atractosoma lombardicum* Brölemann, 1892 (par monotypie).

Syn. :

Ornithogona Cook, 1896 (espèce-type par monotypie : *Atractosoma helveticum* Verhoeff, 1894).

Limnalpium Verhoeff, 1921 (espèce-type désignée par Attems, 1927 : *Atractosoma helveticum* Verhoeff, 1894).

Dorasoma Verhoeff, 1932 (espèce-type désignée ici : *Dorasoma serratum* Verhoeff, 1932).

La plupart des autres noms de genres (cités p. 459 et 460) tels *Ceratosoma, Euceratosoma, Atractosoma, Ochogona, Limnalpium* et *Triakontazona*, qui ont pu épisodiquement abriter tel ou tel taxon de rang spécifique actuellement rapporté au genre *Bomogona*, recouvrent en fait des taxons de rang générique distinct.

Bomogona lombardica (Brölemann, 1892)

Syn. :

Atractosoma lombardicum Brölemann, 1892

Atractosoma lombardicum (Bröl., 1892); Brölemann, 1895

Bomogona lombardica (Bröl., 1892); Cook, 1895
Bomogona lombardicum (Bröl., 1892); Hoffman, 1979
Ceratosoma (*Limnalpium*) *luganensis* Verhoeff, 1921 (syn. nov.)
Ceratosoma (*Limnalpium*) *luganensis ruscorum* Verhoeff, 1921 (syn. nov.)
Ceratosoma (*Limnalpium*) *luganensis* (Verhoeff,1921); Attems, 1927
Ceratosoma (*Limnalpium*) *fontis* Verhoeff, 1932 (syn. nov.)
Asandalum luganense luganense (Verhoeff, 1921); Attems, 1949
Asandalum luganense ruscorum (Verhoeff, 1921); Attems, 1949
Triakontazona (*Limnalpium*) *luganense* (Verhoeff,1921); Strasser, 1978
Ochogona luganensis (Verhoeff, 1921); Strasser et Minelli, 1984
Ochogona luganensis (Verhoeff, 1921); Kurnik, 1986

Bomogona lombardica larii (Verhoeff, 1921)

Syn. :
Ceratosoma (*Limnalpium*) *larii* Verhoeff, 1921
Ceratosoma (*Limnalpium*) *larii* (Verhoeff, 1921); Attems, 1927
Asandalum larii (Verhoeff, 1921); Attems, 1949
Ochogona larii (Verhoeff, 1921); Strasser et Minelli, 1984

Bomogona* (*Ornithogona*) *helvetica (Verhoeff, 1894)

Syn. :
Atractosoma helveticum Verhoeff, 1894
Ornithogona helvetica (Verhoeff, 1894); Cook, 1895
Triakontazona helvetica (Verhoeff, 1894); Verhoeff, 1897
Atractosoma helveticum dentatum Faës, 1902
Ceratosoma (*Triakontazona*) *verbani* Verhoeff, 1910
Ceratosoma (*Limnalpium*) *helveticum* (Verhoeff, 1894); Verhoeff, 1921
Ceratosoma (*Limnalpium*) *verbani* (Verhoeff, 1910); Verhoeff, 1921 (syn. nov.)
Ceratosoma (*Limnalpium*) *verbani* (Verhoeff, 1910); Attems, 1927
Ceratosoma (*Limnalpium*) *helveticum* (Verhoeff, 1894); Attems, 1927
Dorasoma quercuum Verhoeff, 1932 (syn. nov.)
Dorasoma serratum Verhoeff, 1932 (syn. nov.)
Dorasoma helveticum (Verhoeff, 1894); Verhoeff, 1936
Asandalum quercuum (Verhoeff, 1932); Attems, 1949
Asandalum verbani (Verhoeff, 1910); Attems, 1949
Dorasoma helveticum quercuum (Verhoeff, 1932); Strasser, 1978
Ornithogona helvetica (Verhoeff, 1894); Strasser et Minelli, 1984
Ochogona verbani (Verhoeff, 1910); Strasser et Minelli, 1984

V. Chorologie

1. *Bomogona lombardica*

Localités déjà publiées : a) par Brölemann (1892 et 1895) : Italie, Lombardie, Varese : Vedano-Olona et Gavirata, 10.1887 (4 mâles, 1 femelle jeune, 3 exemplaires). Italie, Lombardie, Como : Lecco, 31.07.1892 (1 mâle jeune, 10 jeunes). Italie, Lombardie : Erba, 29.08.1891 (1 mâle, 1 mâle j., 1 exemplaire). Italie, Lombardie, Varese : Val Ganna, 8.02.1888 (1 femelle j., coll. Brölemann). — b) par Verhoeff (1921, 1932, 1936) et Strasser (1978) : Suisse, Tessin : Melide. Italie, Lombardie : Como. Italie, Piémont : Torre Pellice. Italie, Piémont : Ceres. Italie, Piémont : Ala di Sura. Italie, Piémont : Pinerolo. Italie, Piémont : Barge. Italie, Piémont : Lombardore. Italie, Piémont : Torre del Colle. Italie, Emilie-Romagne : Borgotaro.

Matériel inédit de A. Pedroli [les dates précises indiquent les chasses à vue, les périodes indiquent les piégeages (Barber)] : Suisse, Tessin : Monte Generoso (1200-1600 m), 5.11.1983 (5 mâles, 6 femelles). Suisse, Tessin : Stabio (370 m), 9.11.1985 (1 mâle), 14.04.1986 (1 femelle), hiver 1985-1986 (4 mâles, 11 femelles dont 2 leg. A. P. au MNHN Paris, coll. Myriapodes DA 080). Suisse, Tessin : Melide (280 m), 16.09.1984 (2 femelles), 21.04.1985 (1 mâle), hiver 1985-1986 (1 mâle). Suisse, Tessin : Mendrisio, Piona (920 m, versant sud du Monte Generoso), automne-hiver 1988 et 1989 (5 mâles, 13 femelles leg. Lörtscher).

Autres matériels : Suisse, Tessin : Lugano, 16.03.1890, coll. Brölemann (inédit!) (1 mâle, MNHN Paris, coll. Myriapodes DA 080).

2. ***Bomogona lombardica larii***

Localités publiées : a) par Brölemann (1892) (*Atractosoma lombardica*) : Italie, Lombardie, Como : Monte Resegone (près Lecco), 14.08.1892 (1 femelle). — b) par Verhoeff (1921) (*Ceratosoma larii*) : Italie, Lombardie, Como : Bellano (rive orientale). Italie, Lombardie, Como : Rovinata près Lecco (rive orientale).

3. ***Bomogona helvetica***

Localités déjà publiées par Verhoeff (1894), Faës (1902), Verhoeff (1910, 1921, 1932, 1936), Strasser (1978) : Suisse, Valais : Zermatt. Suisse, Valais : Stalden. Suisse, Valais : Visp. Suisse, Valais : Ardon. Suisse, Valais : Mauvoisin. Suisse, Tessin : Bellinzona. Italie, Lombardie : Laveno (rive orientale du lac Majeur). Italie, Aoste : Aoste. [(Italie, Piémont, Novarra : Castelleto s. Ticino) (douteux pour l'un de nous (J.-P. M.)]. Italie, Piémont : Ivrea, Lago Sirio.

Matériel inédit de A. Pedroli (piégeages et chasses à vue) : Suisse, Tessin : Monteggio (260 m, région de la Tresa, vers Ponte Cremenaga), automne/hiver/printemps 1984-1985 (3 mâles, 6 femelles). Suisse, Tessin : Malpenza (270 m, région de Ponte Tresa), printemps 1984 (2 femelles). Suisse, Tessin : Caviano, Ranzo (260 m, lac Majeur), printemps et hiver 1984 (1 mâle, 1 femelle). Suisse, Tessin : Biasca, Loderio (354 m), septembre 1980 (1 mâle, 1 femelle). Suisse, Tessin : Lucomagno, Samprou (1870 m), printemps et automne 1985 (2 mâles, 1 femelle) et 14.9/9.11.1985 (1 femelle, léguée au MNHN Paris, coll. Myriapodes DA 140). Suisse, Tessin : Melera, Val Morobbio (1020 m, région de Bellinzona), automne/hiver/printemps 1988-1989 (61 mâles, 50 femelles, 1 j., leg. Lörtscher). Suisse, Tessin : Prugniasco, Negrentino (870 m, Val Blenio), automne/hiver/printemps 1988-1989 (4 mâles, 8 femelles, 1 j., leg. Lörtscher). Suisse, Tessin : Ludiano, Vala (940 m, Val Blenio), automne/hiver 1988-1989 (3 mâles, 5 femelles, leg. Lörtscher). Suisse, Tessin : Largario, Brinzosca (1000 m), automne/hiver/printemps 1988-1989 (6 mâles, 15 femelles, leg. Lörtscher). Suisse, Tessin : Meride, San Giorgio (1080 m), automne/hiver 1988 (2 mâles, 6 femelles, leg. Lörtscher). Suisse, Tessin : Lavertezzo, Rondana (860 m, Valle Maggia), printemps 1988 (1 mâle, leg. P. Pronini). Suisse, Tessin : Biasca, Val Pontirone (840-1340 m), printemps et automne 1988 (4 mâles, 5 femelles, leg. P. Pronini). Suisse, Tessin : Bodio, 22.4/7.6.1984 (1 femelle MNHN Paris, coll. Myriapodes DA 140). Suisse, Grisons : Leggia (320 m, région de la Moesa), 28.9.1989 (1 mâle). Suisse, Valais : Champex (1466 m, bord du Lac), 26.9.1987 (2 mâles). Suisse, Valais : Val des Dix, Le Chargeur (2100 m), 21.9.1987 (1 mâle).

Autres matériels : Suisse, Tessin : 1 km au nord d'Acquarossa, 5.11.1982, coll. & leg. D. Kime (1 mâle, MNHN Paris, coll. Myriapodes DA 140). Italie, Lombardie : Novarra, Pella (Lago d'Orta), mars 1971, coll. Rosa (1 mâle, Museo Scienze Naturale, Bergamo). Italie, Lombardie : Santa Catarina del Sasso (rive orientale du lac Majeur), 14.10.1888, coll. Brölemann (inédit!) (I mâle, MNHN Paris, coll. Myriapodes DA 140).

Conclusion — Discussion

L'analyse de la distribution géographique, illustrée par la carte (fig. 19), montre que *Bomogona helvetica* a une aire de répartition en position plus externe (et septentrionale) dans

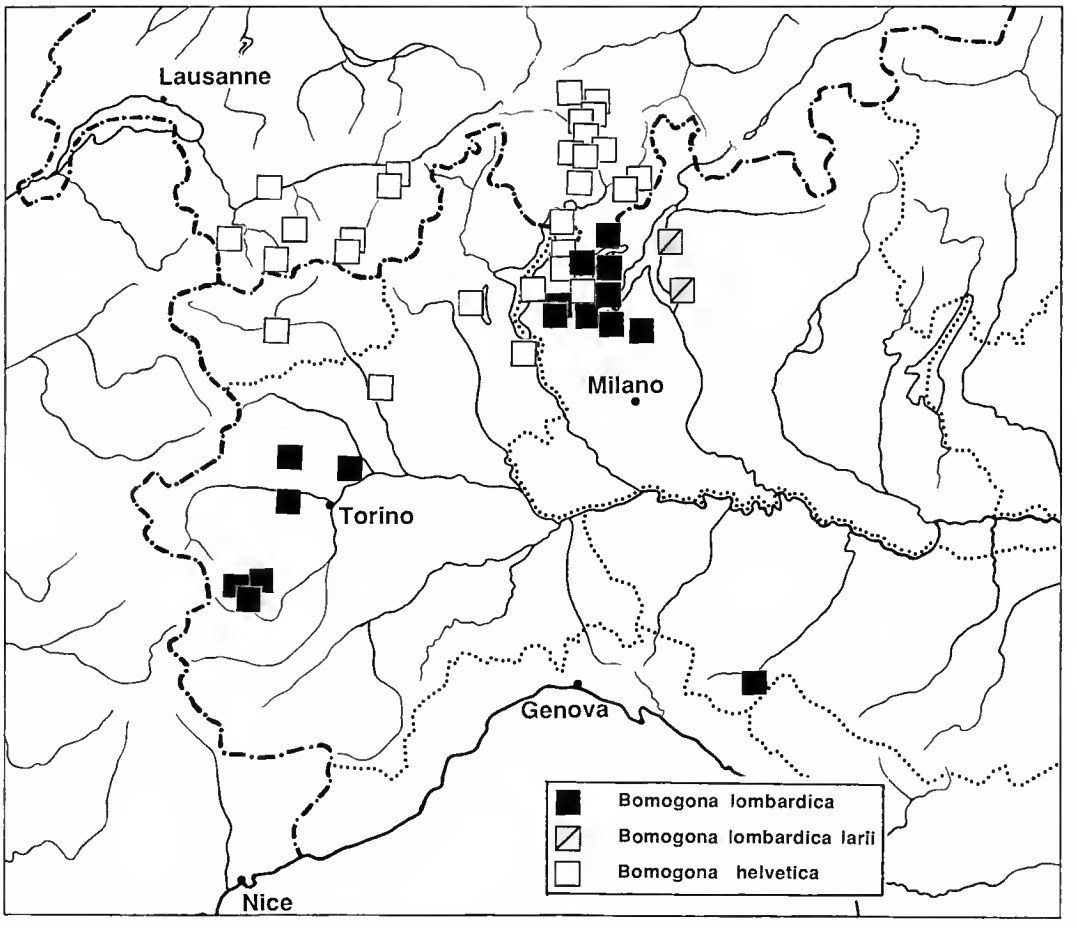

FIG. 19. — Répartition géographique des deux espèces du genre *Bomogona*.

l'arc alpin que *Bomogona lombardica*. Ceci est en harmonie avec le gradient altitudinal des deux espèces; car en effet si toutes deux se rencontrent dès 260 m d'altitude, la première parvient à 2600 m, tandis que la seconde ne dépasse pas 1600.

En Suisse, *lombardica* ne se trouve que dans l'extrême sud du Tessin, dans la région du Monte Generoso, réputé être un massif-refuge, et dans la plaine avoisinante. Dans cette région, la distribution des deux espèces est continue, et il n'y a pas de chevauchement de leurs aires de distribution. Un phénomène semblable a pu être observé chez d'autres Diplopodes; ainsi dans le nord des Alpes et dans le Jura suisse il a été observé sur deux taxons du genre *Rhymogona, R. montivaga* et *R. cervina*; ces deux espèces parapatriques présentent cependant une zone de contact de quelques centaines de mètres à 5 km de large, où se rencontrent des hybrides, ce qui peut faire douter de leur statut d'espèces (PEDROLI-CHRISTEN & SCHOLL, 1990

et 1991). Chez *Bomogona*, on n'a encore rien observé de semblable, mais le phénomène n'est pas à exclure, tant que l'on n'aura pas prospecté minutieusement certaines zones : par exemple celle qui sépare les massifs-refuges du Monte Generoso et du Monte San Giorgio, qui sont occupés respectivement par *B. lombardica* et *B. helvetica* et dont les flancs ne sont séparés que par de faibles distances (1-2 km).

D'autre part, il est assez frappant de constater, à l'examen de la carte, que si *B. helvetica* présente une aire relativement petite avec chorologie relativement homogène, il n'en est pas de même de *B. lombardica*. La chorologie discontinue de cette dernière, qui ne peut s'expliquer entièrement par des défauts de recensement (en trois aires : une aire tessino-lombarde, une aire piémontaise et un isolat nord-apennin), est typique d'une espèce en régression ayant eu autrefois une aire plus vaste; le fait (à confirmer) que ses deux aires principales (tessino-lombarde et piémontaise) sont séparées par une large zone qui est occupée, au moins partiellement, par *helveticum*, tendrait au contraire à nous laisser penser que, à la différence de ce qui se passe chez *Rhymogona, Bomogona helveticum* aurait tendance à supplanter *lombardicum* plutôt qu'à produire des hybrides avec elle.

Remerciements

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Biogéographie des espèces du groupe naturel « *Tityus clathratus* » (Chelicerata, Scorpiones, Buthidae)

par Wilson R. Lourenço

Résumé. — Une nouvelle synthèse biogéographique est proposée pour les onze espèces associées au groupe naturel de Scorpions défini en tant que « *Tityus clathratus* ». Les modèles actuels de distribution et de différenciation sont discutés à partir de considérations fondées sur des facteurs historiques et écologiques.

Abstract. — A new biogeographic synthesis is proposed to the eleven species associated to the natural group of scorpions defined as '*Tityus clathratus*'. The present patterns of distribution and differentiation are discussed taking in consideration the influence of historical and ecological factors.

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Introduction

Le genre *Tityus* (famille des Buthidae) est celui qui présente la plus importante richesse spécifique parmi les genres mondiaux de Scorpions; plus d'une centaine d'espèces sont répertoriées. Le seul travail monographique qui ait traité de la totalité des espèces connues, à l'époque de sa rédaction, est celui de Mello-Leitão (1945). Ce travail est cependant très désactualisé tant sur le plan de la nomenclature que sur le plan du concept de l'espèce et ne présente plus guère qu'un intérêt historique.

Face à la très grande difficulté présentée par le genre *Tityus* pour toute étude globale concernant sa phylogénie et sa biogéographie, plusieurs auteurs ont entrepris des études partielles sur un nombre limité d'espèces du genre, soit par régions géographiques (Maury, 1979; Gonzalez-Sponga, 1984), soit en partant de la définition de groupes naturels d'espèces à l'intérieur du genre (Lourenço, 1984*a*, *b*, 1987*a*; Lourenço et Eickstedt, 1987).

A présent, on constate qu'aucune de ces approches ne semble satisfaisante, en l'absence d'une réelle analyse portant sur la totalité des éléments d'un groupe naturel donné, associée à des études sur les milieux naturels dans lesquels ils habitent.

Une analyse globale du genre *Tityus* a été entreprise par nos soins depuis une quinzaine d'années; non encore terminée, elle se fonde sur des bases évolutives, écologiques et biogéographiques. Ainsi, l'approche présentée ici n'est qu'une partie de ce travail en préparation, qui porte sur un groupe naturel désormais bien défini : le groupe naturel

d'espèces « *Tityus clathratus* ». Ce groupe a déjà fait l'objet d'une étude partielle par LOURENÇO (1984*a*). Depuis, d'autres espèces appartenant à ce groupe ont été décrites (FRANCKE et STOCKWELL, 1987; LOURENÇO, 1991), et une nouvelle espèce se rattachant à ce groupe est décrite dans la présente note.

Tityus betschi n. sp.

(Fig. 1 à 4)

MATÉRIEL-TYPE : Holotype femelle : Colombie, Depto. Valle del Cauca; Parque Nacional Farallones de Cali (Cerca a Pance, 1450 m alt., en techo de un rancho rural), IX, 1988, leg. E. FLOREZ. Muséum national d'Histoire naturelle, Paris, MNHN-RS-8552.

ÉTYMOLOGIE : Le nom spécifique est créé en hommage à notre collègue le Dr. Jean-Marie BETSCH du Muséum national d'Histoire naturelle, Paris.

DESCRIPTION

Coloration générale jaunâtre avec des taches châtain brunâtre. Prosoma jaunâtre avec des taches brunâtres diffuses; tubercule oculaire et yeux latéraux noirâtres. Mesosoma : tergites I

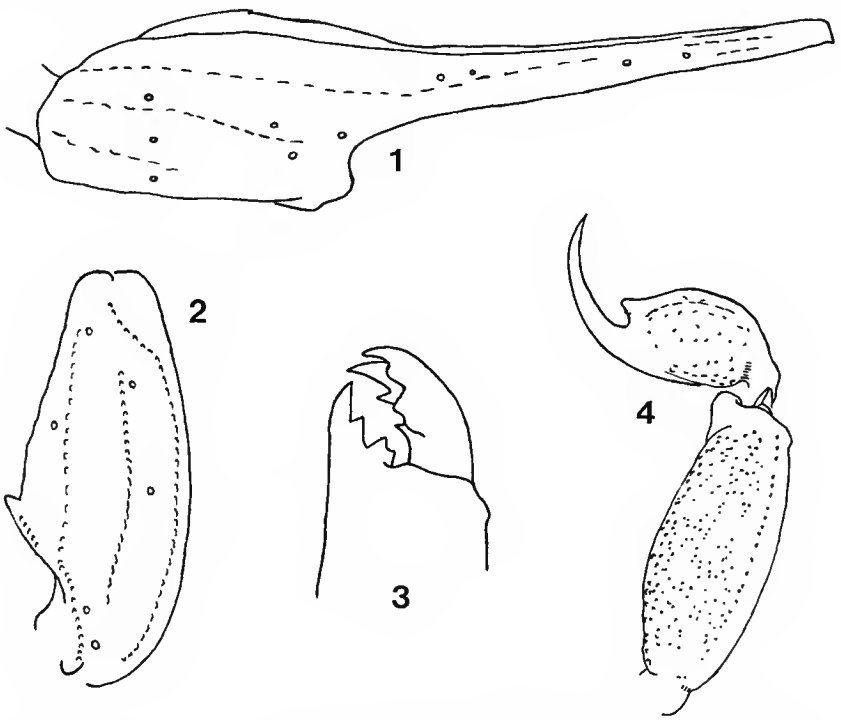

FIG. 1 à 4. — *Tityus betschi*, holotype ♀ : 1, pince, vue externe; 2, tibia, vue dorsale; 3, chélicère; 4, V^{e} anneau du métasoma et telson, vue latérale.

à VII avec le même dessin que la plaque prosomienne. Sternites jaune brunâtre avec des taches diffuses dans la région postérieure de chaque sternite. Metasoma : anneaux caudaux I à V jaunâtres, avec des taches brunâtres plus diffuses que celles du prosoma et du mesosoma. Telson jaune rougeâtre avec des taches très estompées. Peignes, opercule génital, sternum, hanches et processus maxillaires ocre-jaune. Pattes et pédipalpes jaunâtres, avec des taches brunâtres diffuses. Chélicères jaunâtres avec des taches noires dans sa partie antérieure.

Prosoma : front de la plaque prosomienne avec une échancrure frontale moyennement marquée. Tubercule oculaire antérieur par rapport au centre de la plaque prosomienne ; yeux médians séparés par plus d'un diamètre oculaire ; trois paires d'yeux latéraux. Plaque prosomienne faiblement granulée ; carènes médianes oculaires allant du bord antérieur jusqu'en arrière du tubercule oculaire ; carènes médianes postérieures moyennement marquées ; sillon interoculaire bien marqué.

Mesosoma : tergites moyennement granulés ; carène axiale présente sur tous les tergites ; tergite VII avec cinq carènes, l'axiale limitée au tiers antérieur ; les deux médianes et les deux latérales fusionnées dans la région proximale. Sternites très peu granulés ; stigmates linéaires. Peignes avec 13-13 dents ; lame basilaire intermédiaire non dilatée.

Metasoma : anneau I avec 10 carènes ; anneaux II à IV avec 8 carènes ; anneau V avec 5 carènes ; espaces intercarénaux faiblement ou moyennement granulés ; vésicule peu granulée ; épine sous-aiguillonnaire rhomboïdale et importante, avec deux granules ventraux.

Pédipalpes : fémur à 5 carènes, tibia à 7 carènes, la carène interne-dorsale à granules spiniformes. Pince avec 9 carènes. Tranchant des doigts mobiles avec 14-14 séries de granules. Chélicères avec la dentition comme chez d'autres *Tityus*. Trichobothriotaxie : A-Alpha, orthobothriotaxique.

Mensurations (en mm) *de l'exemplaire décrit* : Prosoma, longueur 4,2 ; largeur antérieure 2,9. Anneau caudal I, longueur 2,6 ; largeur 2,1. Anneau caudal V, longueur 5,2 ; largeur 1,7 ; hauteur 1,8. Vésicule, largeur 1,6 ; hauteur 1,5. Pince, largeur 1,6 ; hauteur 1,4. Doigt mobile, longueur 5,3.

Biogéographie des espèces du groupe naturel « *Tityus clathratus* »

Au total onze espèces peuvent être incluses dans le groupe naturel « *Tityus clathratus* ». Elles sont réparties en trois sous-groupes selon leurs affinités phylogénétiques et selon leurs « patterns » de distribution géographique.

Premier sous-groupe :

— *Tityus paraguayensis* Kraepelin, habitant du chaco, formation végétale ouverte semi-xérophytique de la région méridionale de l'Amérique du Sud (Lourenço, 1990) ;

— *Tityus mattogrossensis* Borelli, espèce des cerrados du centre du Brésil (Lourenço, 1979).

DEUXIÈME SOUS-GROUPE :

— *Tityus pusillus* Pocock, endémique de la région nord de la forêt atlantique du Brésil, dans l'État de Pernambuco (LOURENÇO, 1982);

— *Tityus silvestris* Pocock et *Tityus bastosi* Lourenço, deux espèces à distribution fondamentalement amazonienne; la première est répartie sur l'ensemble de l'Amazonie, avec une légère pénétration sur la région guyanaise (LOURENÇO, 1988*a*); la deuxième est présente sur la région occidentale de l'Amazonie (LOURENÇO, 1984*a*);

— *Tityus clathratus* Koch, à distribution typiquement guyanaise qui déborde légèrement sur les îles continentales du Vénézuela, et *Tityus atriventer* Pocock, endémique de l'île de Grenade (LOURENÇO, 1984*c*); ces deux espèces sont des vicariantes.

TROISIÈME SOUS-GROUPE :

— *Tityus columbianus* (Thorell) et *Tityus betschi* n. sp., deux espèces vicariantes; elles habitent respectivement des savanes d'altitude et des forêts sèches de semi-altitude en Colombie;

— *Tityus tayrona* Lourenço et *Tityus ocelote* Stockwell et Francke; la première espèce habite les forêts humides de Santa Marta en Colombie (LOURENÇO, 1991); la deuxième est connue des forêts humides du Costa Rica.

Il va de soi que le présent inventaire des espèces du groupe naturel « *Tityus clathratus* » ne peut encore être considéré comme définitif.

Au vu de la très grande homogénéité morphologique des espèces du groupe, une analyse phylogénétique précise s'avère très difficile; la caractérisation des apomorphies et des plésiomorphies apparaît comme peu réalisable à partir des seuls caractères morphologiques généraux. De ce fait, la définition des sous-groupes est également fondée sur d'autres caractères que ceux tirés de la morphologie, avec une tentative d'optimisation des données écologiques et biogéographiques (tabl. I).

Les « patterns » actuels de répartition et de différenciation des espèces du groupe « *Tityus clathratus* »

La figure 5 représente la répartition actuelle connue des onze espèces associées au groupe « *T. clathratus* ». L'évolution même des aires de répartition des diverses espèces est conséquence à la fois des facteurs historiques responsables de l'évolution de la région mais aussi des stratégies adaptatives (facteurs écologiques) spécifiques de chacune des espèces (tabl. I).

Les Scorpions correspondent en général à des souches génétiques anciennes; ainsi, on peut estimer que le groupe « *T. clathratus* » correspond à une lignée existant déjà depuis le Tertiaire supérieur au moins (SCHWALLER, 1982).

Comme tous les *Tityus*, ceux du groupe « *T. clathratus* » ont leur centre d'origine en Amérique du Sud; cependant, on ne peut encore affirmer lequel des deux boucliers, guyanais ou brésilien (HAFFER, 1981), a été le foyer d'origine du groupe au cours du Tertiaire.

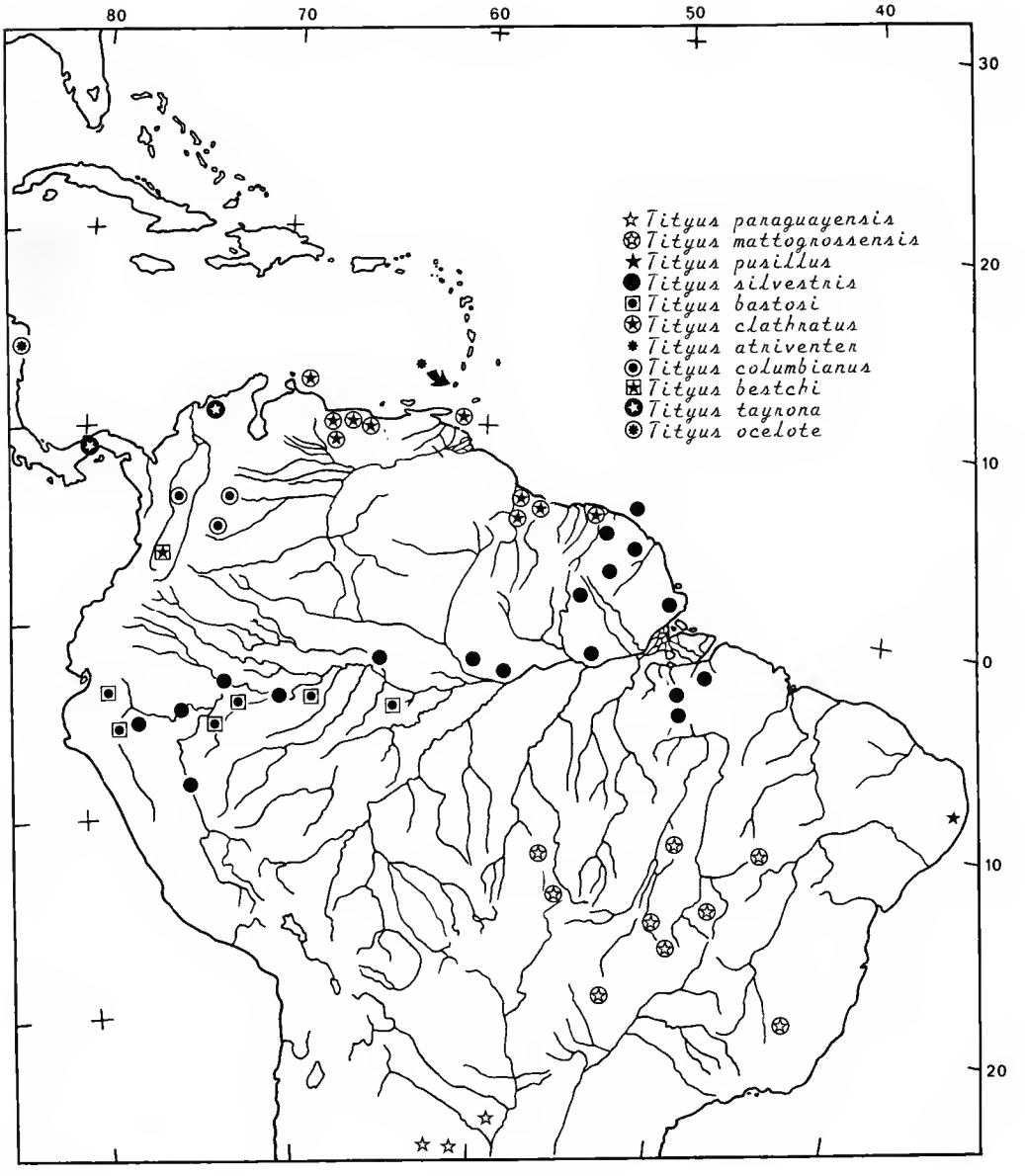

FIG. 5. — Répartition géographique des espèces du groupe « *T. clathratus* ».

TABLEAU I. — Caractéristiques écologiques et biologiques des espèces du groupe « *T. clathratus* ».

ESPÈCE	HABITAT	MICRO-HABITAT	MORPHOLOGIE	BIOLOGIE REPRODUCTRICE
T. mattogrossensis	cerrado	s/termitières, bois, pierres; dans palmiers	monomorphe	sexuée
T. paraguayensis	chaco	s/bois	monomorphe	sexuée
T. pusillus	forêt humide	s/pierres; litière	monomorphe	sexuée
T. silvestris	forêt humide	dans litière et palmiers	polymorphe; ochlospecies	sexuée
T. bastosi	forêt humide	dans litière	polymorphe; ochlospecies	sexuée
T. clathratus	forêt humide et sèche	dans litière; s/bois	polymorphe; cline	sexuée
T. atriventer	forêt humide	dans litière; s/bois	monomorphe	sexuée
T. tayrona	forêt humide	dans litière; s/bois	monomorphe	sexuée
T. ocelote	forêt humide	dans litière	monomorphe	sexuée
T. columbianus	savane d'altitude	s/pierres	monomorphe	sexuée et parthenogénétique
T. betschi	forêt sèche	s/bois	monomorphe	sexuée

Les parentés phylogénétiques sont en général corrélées avec les distributions géographiques, voire avec certains traits de l'écologie des espèces (tabl. I). Les aspects suivants peuvent être mis en évidence :

— *Tityus mattogrossensis* et *Tityus paraguayensis* sont des espèces habitant exclusivement des formations végétales ouvertes du type savanicole, dans les régions centrale et méridionale d'Amérique du Sud.

— *Tityus pusillus*, endémique de la région nord de la forêt atlantique, a dû s'isoler des espèces amazoniennes par suite de la disparition des ponts entre les deux forêts humides (ANDRADE-LIMA, 1982; LOURENÇO, 1988*b*).

— *Tityus clathratus*, espèce adaptée aux forêts humides dans la région guyanaise, affiche une répartition disjointe; les populations que l'on retrouve au nord du Vénézuela et sur ses îles continentales habitent des milieux forestiers beaucoup plus secs (fig. 5).

— *Tityus atriventer*, espèce vicariante de *T. clathratus*, est le résultat d'une dispersion du groupe vers les Antilles avec différenciation postérieure due à son isolement dans l'île de Grenade. Cette dispersion a probablement eu lieu au cours des très importantes glaciations du Quaternaire; pendant cette période, le niveau des mers a connu de très importantes réductions, de l'ordre de 100 à 150 m (LOURENÇO, 1987*b*); de ce fait, la distance entre l'Amérique du Sud et l'île de Grenade fut réduite de 125 km à environ 30 km, du fait de l'émersion des bancs (GRIFFITHS et KLINGENER, 1988).

— *Tityus silvestris* et *Tityus bastosi* sont des espèces à large répartition sur l'Amazonie; elles affichent toutes les deux un polymorphisme du type ochlospecies (LOURENÇO, 1988). Cette variabilité génétique, exprimée morphologiquement, met en évidence, lorsqu'elle est corrélée avec les « patterns » de distribution, des caractéristiques d'une colonisation « récente » du bassin amazonien, qui a dû se réaliser progressivement à la suite de la réexpansion de la forêt

humide après l'événement du dernier épisode sec. En outre, si l'hypothèse de l'existence d'un grand lac sur le bassin amazonien dans des périodes récentes est retenue (cf. Lago Amazonas), la colonisation de cette région par les deux espèces ne peut être datée que postérieurement à la disparition du lac en question (FRAILEY *et al.*, 1988; MORI, 1991).

— *Tityus columbianus* et *T. betschi* habitent dans des milieux secs respectivement savanicoles et forestiers dans les cordillères occidentale et orientale de Colombie.

— *Tityus tayrona* et *Tityus ocelote* habitent des milieux du type forêt humide. La première espèce aurait pu se différencier dans le centre d'endémisme Santa Marta en Colombie (LOURENÇO, 1991), tandis que la deuxième a pu subir sa différenciation au Costa Rica en Amérique centrale, par suite de la dispersion et de la colonisation de cette région par des éléments du groupe en association avec des périodes d'isolement.

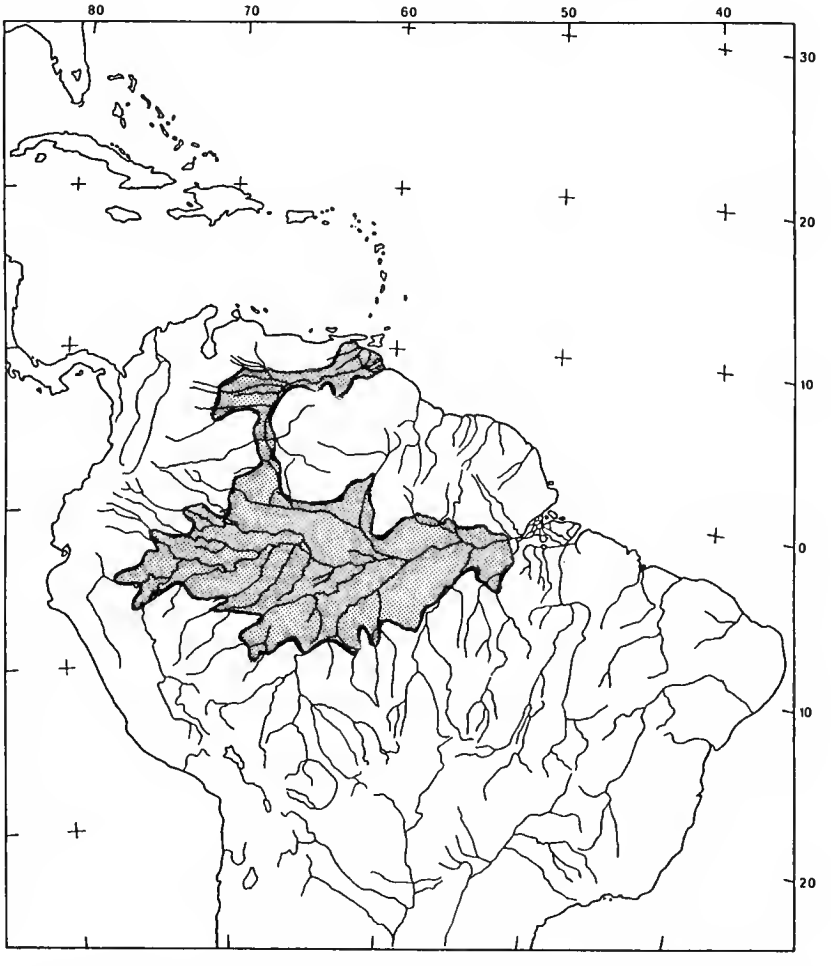

FIG. 6. — L'étendue du « Lago Amazonas » d'après FRAILEY *et al.* (1988).

Conclusions

Si *Tityus mattogrossensis* et *Tityus paraguayensis* sont des espèces adaptées à des formations végétales ouvertes, partiellement xérophytiques, elles sont néanmoins séparées par une barrière représentée par le « Pantanal » du Mato Grosso, zone beaucoup plus humide et inondée annuellement ; cette barrière écologique est ainsi très efficace.

Tityus pusillus est endémique de la forêt atlantique située sur la région côtière de l'État de Pernambuco au Brésil. La très vaste dégradation de cette forêt impose un net recul des populations animales jusqu'à leur totale disparition (Prance et Campbell, 1988). Cette espèce très menacée d'une disparition totale a dû avoir jadis une répartition plus importante.

La distribution disjointe de *Tityus clathratus* pourrait être expliquée à partir de la théorie du « Lago Amazonas » qui aurait existé à la fin du Pléistocène et au début de l'Holocène (fig. 6). En fait, l'étendue de ce lac, proposée par Frailey *et al.* (1988), recouvre bien la zone de disjonction dans la distribution actuelle de *T. clathratus*.

En se fondant également sur l'hypothèse du « Lago Amazonas », il est possible de postuler que les répartitions actuelles de *Tityus silvestris* et de *Tityus bastosi* sont les plus récemment établies, parmi celles des espèces du groupe « *T. clathratus* » ; elles sont très probablement encore en voie d'expansion. La condition d'ochlospecies est en général en corrélation avec les caractéristiques d'une différenciation et d'une distribution récentes (Prance, 1982 ; Lourenço, 1988*a*).

Les différenciations de *Tityus tayrona, Tityus columbianus* et de *Tityus betschi* semblent être associées à des refuges quaternaires qui se sont retrouvés isolés à plusieurs reprises au cours de l'alternance des épisodes secs et humides (Lourenço, 1986 ; Lourenço et Florez, 1990).

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Présence du genre *Bathynarius* (Crustacea, Decapoda, Diogenidae) en Indonésie et dans le Pacifique central, avec la description de deux espèces nouvelles

par Jacques FOREST

Résumé. — Le genre d'eau profonde *Bathynarius*, récemment établi avec deux espèces incluses, s'agrandit avec la description de *B. wolffi* et *B. pacificus* spp. nov. Sa distribution géographique, jusqu'à présent restreinte à la mer des Antilles et à l'océan Indien, se trouve étendue à l'Indonésie et à la Polynésie. La capture dans cette dernière région de plusieurs spécimens de l'espèce de l'océan Indien, *B. albicinctus* (Alcock), a permis de compléter la comparaison avec *B. anomalus* (A. Milne Edwards et Bouvier). Diagnose et définition ont été amendées en fonction des particularités des nouveaux taxa et une clef d'identification est fournie pour les quatre espèces.

Abstract. — The deep sea genus *Bathynarius*, recently established with two included species, is enlarged by the description of two further species, *B. wolffi* and *B. pacificus* spp.nov. Its geographical distribution, until now restricted to the Caribbean Sea and Indian Ocean, is extended to Indonesia and Polynesia. The capture in this last area of several specimens of the Indian species, *B. albicinctus* (Alcock), enables a full comparison with the Western Atlantic species *B. anomalus* (A. Milne Edwards et Bouvier). The diagnosis and definition of the genus are amended in accordance with the particularities of the new taxa and an identification key is provided for the four species.

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Le genre *Bathynarius* a été récemment établi (FOREST, 1989 : 759) pour deux espèces précédemment rangées dans le genre *Clibanarius* Dana. La première, *B. anomalus* (A. Milne Edwards et Bouvier, 1893), vit dans les parages des Petites et Grandes Antilles, alors que la seconde, *B. albicinctus* (Alcock, 1905), décrite du sud de l'Inde, n'avait été retrouvée qu'au large de l'île de La Réunion. Étroitement apparentées, en dépit de leur éloignement géographique, les deux espèces se distinguent par une coloration fort différente.

Les *Bathynarius* et les *Clibanarius* ont en commun un habitus assez voisin, ce qui explique les confusions antérieures, mais sont en fait sans affinités réelles. Ils ont aussi une distribution tout à fait différente : les premiers vivent en eau profonde, alors que les *Clibanarius* se tiennent dans la zone intertidale ou à proximité.

Le genre *Bathynarius* s'enrichit aujourd'hui de deux nouvelles espèces et en même temps sa distribution géographique s'élargit considérablement. Il est en effet représenté parmi les nombreux et intéressants crustacés recueillis par J. POUPIN en Polynésie française, dans le cadre des activités du Service Mixte de Contrôle Biologique des Armées. Il s'agit d'abord d'un échantillon de onze spécimens capturés en même temps dans des nasses aux îles Marquises, par

210 m de profondeur. L'un de ces spécimens est indiscutablement identifiable à *B. albicinctus* qui, nous l'avons dit, n'était connu que de deux localités de l'océan Indien, alors que les dix autres appartiennent à une nouvelle espèce décrite ici sous le nom de *B. pacificus* sp. nov. Un second échantillon, provenant celui-là des îles Tubuaï, comprend seize *B. albicinctus*, et un spécimen unique recueilli aux Tuamotu appartient à la même espèce. Enfin, les pagures du Zoologiske Museum de Copenhague, qui m'ont été confiés par le Dr. Torben WOLFF, incluent également un spécimen d'un autre *Bathynarius* nouveau provenant des récoltes du Dr. Th. MORTENSEN aux îles Kei : *B. wolffi* sp. nov.

La présente note comporte la description des deux nouvelles espèces et des remarques sur leurs affinités et leur distribution, ainsi que des données complémentaires sur *B. albicinctus*, grâce à l'examen d'un assez grand nombre d'exemplaires. Mes observations précédentes sur l'espèce d'ALCOCK portaient essentiellement sur un spécimen unique (FOREST, 1989 : 770). En le comparant aux nombreux *B. anomalus* disponibles, j'avais noté de minimes différences dont la signification spécifique restait douteuse, dans l'ignorance des variations morphologiques possibles d'*albicinctus*. Le nouveau matériel obtenu confirme que les deux espèces sont proches, tout en se distinguant non seulement par la coloration, mais aussi par une série de caractères principalement liés à l'ornementation.

Des remarques complémentaires sont également présentées sur les caractères du genre *Bathynarius*. En effet, si les deux espèces décrites ici offrent les principaux traits morphologiques auxquels avait été accordée une signification générique, certaines de leurs particularités ont montré que définition et diagnose nécessitaient quelques corrections.

Chaque fois que la taille d'un spécimen est précisée, il s'agit de la longueur de l'écusson céphalothoracique sur son axe médian. En effet, la longueur de la carapace entre le sommet du rostre et soit l'échancrure médiane (comme dans mes précédentes publications), soit le bord des lobes branchiaux, est sujette à de fortes fluctuations pour un écusson de longueur donnée, en raison de la nature membraneuse et de l'absence de rigidité des téguments au niveau de la partie postérieure du céphalothorax.

Bathynarius albicinctus (Alcock, 1905)

(Fig. 2, 7, 10)

Clibanarius albicinctus Alcock, 1905 : 50, pl. 4, fig. 4 ; BUITENDIJK, 1937 : 267 ; FOREST, 1952 : 34 ; FIZE et SERÈNE, 1955 : 69, 70, 74.
Bathynarius albicinctus ; FOREST, 1989 : 768, fig. 2, 3, 6.

MATÉRIEL EXAMINÉ. — **Iles Marquises**, Fatuhiva, Récoltes du Service Mixte de Contrôle Biologique des Armées, station 303, 10°31,4'S, 138°39,2'W, 210 m, nasses, J. POUPIN coll. 03.09.1990 : 1 ♀ 5,5 mm (Pg 4864). — **Archipel des Tuamotu**, Fangataufa, Récoltes du Service Mixte de Contrôle Biologique des Armées, station 322, 22°12,9'S, 138°43,1'W, 250 m, nasses, J. POUPIN coll., 23.10.1990 : 1 ♀ 5,4 mm (Pg 4865). — **Iles Tubuaï**, Rurutu, Récoltes du Service Mixte de Contrôle Biologique des Armées, station 337, 22°28,6'S, 151°21,8'W, 125 m, nasses, J. POUPIN coll., 27.11.1990 : 10 ♂ 4,5 à 8,7 mm, 6 ♀ 5,2 à 7,2 mm, dont 2 ovigères de 5,4 mm et 7,2 mm (Pg 4866).

REMARQUES

Les dix-huit exemplaires de *Bathynarius* des îles Marquises, Tuamotu et Tubuaï mentionnés ci-dessus sont incontestablement identifiables à *B. albicinctus* (Alcock). Ils correspondent à la description originale et présentent les caractéristiques du spécimen de La Réunion étudié lors de l'établissement du genre (FOREST, 1989 : 768), avec en particulier une coloration tout à fait identique. L'examen de ce nouveau matériel donne une idée des variations de l'espèce et permet de préciser ses rapports avec celle des Antilles, *B. anomalus* (A. Milne Edwards et Bouvier). Les deux espèces se distinguent immédiatement par la pigmentation. Les péréiopodes de *B. albicinctus* sont d'un rouge intense piqueté de blanc — teinte à peine atténuée huit ans après la fixation — et marqués de larges anneaux blancs, alors que, chez *B. anomalus*, ces appendices sont d'une teinte rose assez uniforme et fugace.

Les dimensions relatives des pédoncules oculaires, antennulaires et antennaires, sont sensiblement les mêmes chez l'une et chez l'autre, avec des variations d'une même étendue. Le rapport de la longueur des pédoncules oculaires à celle de l'écusson a été calculé chez tous les *B. albicinctus*, qui mesurent de 4,0 à 8,7 mm : il s'échelonne entre 3/4 et 4/5. Quant à l'indice cornéen, c'est-à-dire le rapport de la longueur des pédoncules au diamètre des cornées, il est compris entre 4,3 et 5,4. Ces rapports, indépendants du sexe, apparaissent dans l'ensemble comme liés à la taille : les individus les plus grands ont des pédoncules oculaires relativement plus longs et plus grêles, avec des cornées plus petites. Les mesures effectuées chez *B. anomalus* avaient donné des résultats similaires, avec des variations d'une plus grande amplitude, conséquence de l'examen d'un nombre beaucoup plus élevé d'individus et d'un plus large échelonnement des tailles. En ce qui concerne la forme des pédoncules oculaires, on peut déceler un très léger renflement de la région cornéenne, fréquent chez *albicinctus*, plus rare chez *anomalus*.

La différence, déjà relevée, dans la spinulation des écailles antennaires se trouve confirmée : les dents épineuses, la distale comprise, sont plus longues, plus fines et plus aiguës chez *albicinctus*.

Les chélipèdes offrent des particularités spécifiques, non seulement dans leur ornementation, mais aussi dans la forme et les proportions de la main. Chez *albicinctus* (fig. 2), celle-ci est modérément renflée du côté ventral, le bord latéral présente une convexité légèrement atténuée vers son milieu et la région digitale est de forme ovalo-triangulaire ; la main est près de deux fois plus longue que large et la région digitale occupe les 4/7e de la longueur totale. Chez *anomalus* (fig. 3), la main présente un renflement latéro-ventral marqué, le bord latéral est convexe au niveau de la paume, puis droit ou même légèrement concave, puis faiblement convexe jusqu'à l'ongle ; la région digitale est nettement triangulaire ; la largeur de la main est sensiblement égale aux 3/5e de la longueur totale et les doigts, plus longs, occupent les 3/5e de cette longueur. La face dorsale de la main de *B. anomalus* est couverte de forts tubercules coniques, à sommet le plus souvent corné , aigu ou émoussé. Chez *B. albicinctus*, les tubercules sont un peu plus nombreux mais de taille irrégulière, les plus grands nettement plus petits que chez *anomalus*, et en cônes plus aigus.

Les longueurs relatives des articles des deuxièmes et troisièmes péréiopodes sont à peu près les mêmes chez les deux espèces, avec des variations notables chez l'une et chez l'autre. Ces articles sont cependant nettement plus allongés, plus grêles chez *B. albicinctus* (fig. 7) que chez *B. anomalus* (fig. 6) : ainsi, les rapports de la longueur du propode à sa hauteur maximale pour

les deuxièmes et troisièmes péréiopodes gauches (article toujours nettement plus court sur le second de ces appendices) sont-ils en moyenne respectivement égaux à 3,4 et 3,0 chez *albicinctus*, à 2,7 et 2,4 chez *anomalus*. En outre, la région distale du dactyle est plus fortement recourbée et l'ongle relativement plus long chez *albicinctus*. On observe aussi de fortes variations individuelles dans le développement des denticules cornés sur la région dorsale du carpe, du propode et du dactyle des pattes ambulatoires. Cependant ces denticules sont dans l'ensemble moins forts, avec une base calcifiée souvent réduite et une épine apicale plus fine, chez *B. albicinctus*, où ils sont parfois à peine discernables.

Les deux espèces ont un sixième tergite abdominal à bord postérieur garni de denticulations irrégulières et en nombre variable (fig. 10 et 11). Elles ont l'une et l'autre un telson fortement asymétrique et de forme voisine, mais nettement plus long que large chez *B. albicinctus*, alors que les deux dimensions sont subégales chez *B. anomalus*. Chez le premier, le lobe gauche est très allongé, ses bords ne convergent que faiblement avant de se rejoindre en un parfait arrondi ; chez le second ce lobe est plus court et aussi plus triangulaire. Quant au lobe droit, toujours très arrondi, il est plus court et moins saillant encore chez *B. albicinctus* que chez *B. anomalus*.

B. albicinctus, qui n'était connu que de l'océan Indien — sud de l'Inde et île de La Réunion — voit sa distribution géographique étendue, de façon considérable, à la Polynésie française. A en juger par le nombre d'individus recueillis en une seule station, il est probable qu'elle n'est pas rare dans cette région et qu'elle sera retrouvée ailleurs dans le Pacifique.

C'est à 125 m de profondeur, aux Tubuaï, qu'ont été obtenus les échantillons les plus nombreux, alors que les autres récoltes, avec un ou deux exemplaires seulement, aux Marquises, aux Tuamotu et dans l'océan Indien, ont été faites entre 185 et 250 m.

Bathynarius pacificus sp. nov.

(Fig. 1, 4, 9, 12)

Matériel examiné. — **Iles Marquises**, Fatuhiva, Récoltes du Service Mixte de Contrôle Biologique des Armées, station 303, 10°31,4'S, 138°39,2'W, 210 m, nasses, J. Poupin coll. 03.09.1990 : 8 ♂ 8,1 à 11 mm, 2 ♀ 5 et 6,1 mm.

Type. — Un mâle de 10,5 mm a été désigné comme holotype (MNHN Pg 4867). Les neuf autres spécimens sont des paratypes (Pg 4868).

Localité-type. — Voir ci-dessus.

Coquilles. — *Bursa latitudo wolfei* Ben, *Conus monachus* L., *Morum* sp.nov.

Description

Écusson céphalothoracique (fig. 1) en général nettement plus long que large. Bords latéraux faiblement convexes, avec une indentation peu prononcée en arrière de leur milieu. Rostre en triangle très obtus, à sommet émoussé dépassant les saillies postantennaires qui portent un très petit denticule. Surface de l'écusson marquée de dépressions lui donnant un

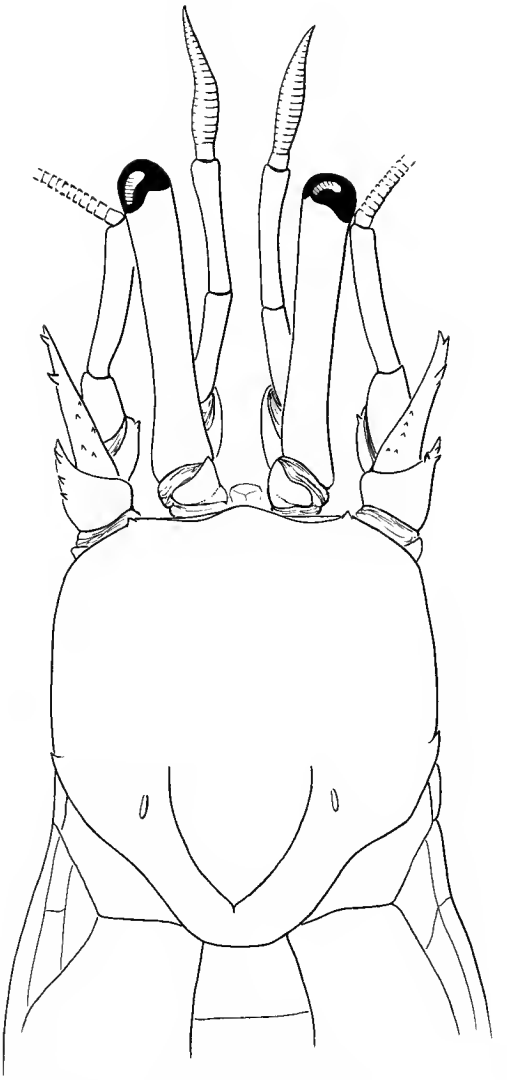

FIG. 1. — *Bathynarius pacificus* sp. nov., SMCB, st. 303 (I. Marquises), mâle holotype 10,5 mm. Région antérieure de la carapace et appendices sensoriels (× 5,5).

aspect corrodé, sauf sur la région gastrique qui est presque lisse. Sur la moitié postérieure de l'écusson deux sillons régulièrement arqués, décalcifiés, convergent vers l'arrière et peuvent se prolonger jusqu'au sillon cervical en une courte ligne médiane. Sur la moitié antérieure, en arrière du rostre les dépressions coalescentes forment une gouttière médiane qui se prolonge par une ligne très fine ; celle-ci, vers le tiers de la longueur de l'écusson, diverge en un Y dont les branches rejoignent ou non les sillons arqués de la moitié postérieure. Ces sillons en Y sont

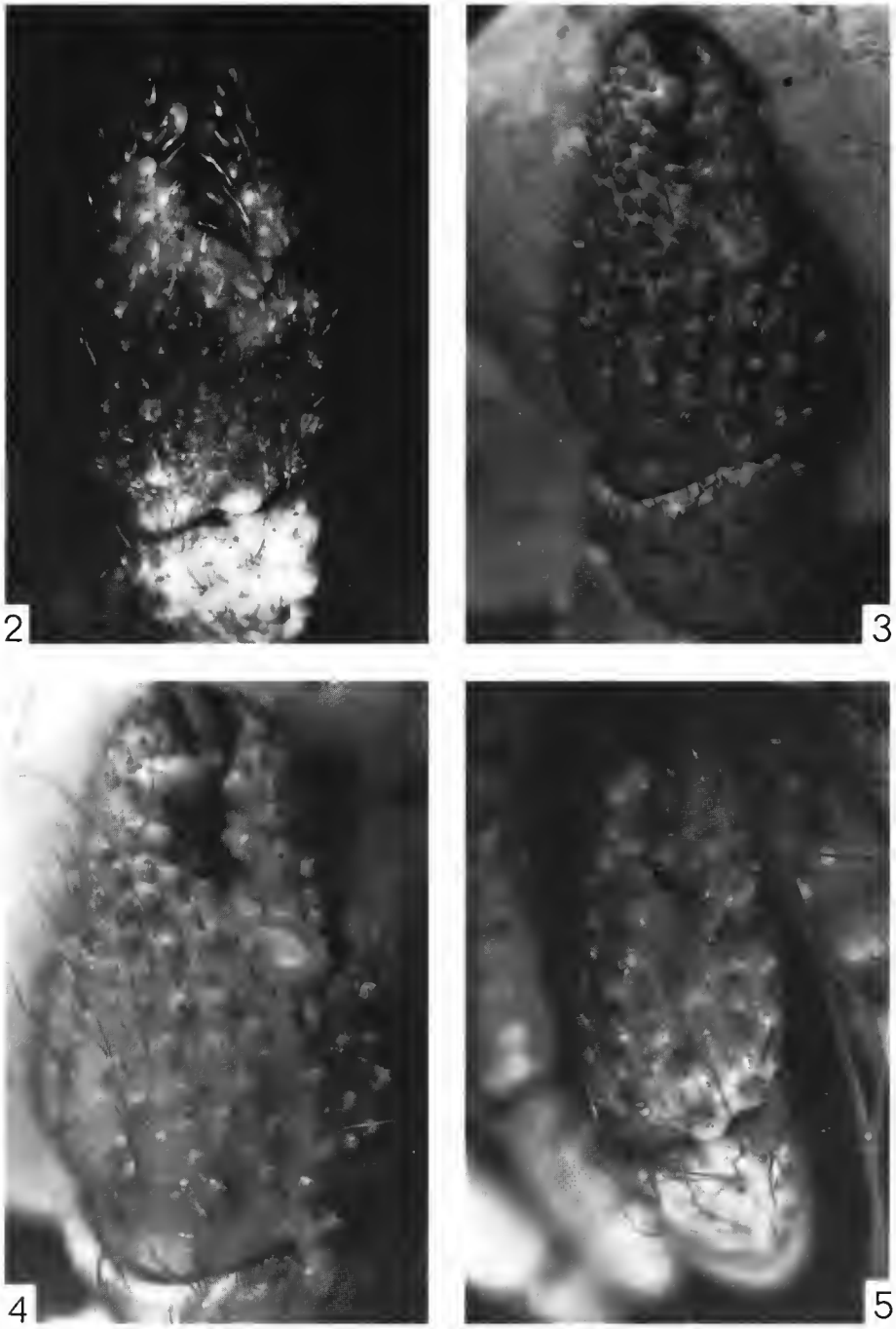

FIG. 2-5 . — Main du chélipède gauche, vue dorsale : 2, *Bathynarius albicinctus* (Alcock), « Marion-Dufresne », camp. MD 32, st. CP 57 (I. de La Réunion), femelle 7,5 mm ; 3, *B. anomalus* (A. Milne Edwards et Bouvier), « Gerda », st. 251 (Floride), mâle 7,6 mm ; 4, *B. pacificus* sp. nov., SMCB, st. 303 (I. Marquises), mâle paratype 9,5 mm ; 5, *B.wolffi* sp. nov., The Danish Expedition to the Kei Islands 1922, st. 3, mâle holotype 5,7 mm.

diversement développés ; ils peuvent être, au moins partiellement, marqués par une ligne décalcifiée ou être atténués, mais sont toujours discernables. Un fin sillon traverse la partie antérieure de la région cardiaque.

Pédoncules oculaires égaux ou un peu plus longs à gauche qu'à droite, subcylindriques, légèrement renflés à la base, leur diamètre minimal compris de 8 à 9 fois dans leur longueur ; celle-ci en moyenne inférieure d'un quart à celle de l'écusson. Cornées hémisphériques, à peine dilatées, le rapport de leur diamètre à la longueur des pédoncules compris entre 5,5 et 6 chez les mâles, plus faible chez les femelles, qui sont plus petites. Écailles oculaires largement séparées, subtriangulaires, à sommet peu aigu parfois obscurément bidenté. Pédoncules antennulaires de même longueur ou légèrement plus longs que les pédoncules oculaires.

Pédoncules antennaires atteignant ou presque la base des cornées. Saillie antéro-latérale du deuxième article robuste, avec quelques denticules en arrière de la pointe distale. Écaille antennaire grêle, atteignant ou dépassant le quart proximal du dernier article pédonculaire, armée d'une ou deux dents latérales assez fortes en arrière de son sommet et de quelques denticules sur sa moitié proximale. Flagelle un peu plus long que la carapace.

Pièces buccales proches de celles de *B. anomalus* (Forest, 1989, fig.5 b, d, g, j, k) et de *B. albicinctus*. Cependant, sur l'endopodite des maxillules le processus flagelliforme latéral est plus fort et les soies distales au nombre de 6 ; sur le mérus des 3e maxillipèdes, il y a 2 ou 3 dents ventrales assez fortes et aiguës, avec parfois 1 ou 2 denticules accessoires.

Chélipèdes semblables et subégaux. Une fissure membraneuse longitudinale sur la face ventrale de la coxa. Mérus robuste, ses faces latérales et mésiales peu convexes, presque planes, bordées de tubercules du côté ventral ; ces faces ont une largeur maximale égale aux deux tiers de la longueur de l'article. Main (fig. 4) à paume renflée, épaisse ; le rapport de sa longueur à sa largeur maximale légèrement inférieur à 2. Région digitale à peu près aussi longue que la région palmaire. Sur la face dorsale de la main des dents coniques, à sommet corné, dont le développement et l'arrangement sont assez variables : elles ne sont jamais très fortes ni très denses, n'ont pas une distribution homogène et ne sont pas alignées, mais sont relativement plus grandes et plus rapprochées sur les portions dorso-latérale (avec une extension sur le doigt fixe) et dorso-mésiale de la paume. Sur le bord préhensile du doigt fixe, une dent molariforme volumineuse empiète légèrement sur l'ongle corné. La portion latérale renflée de la paume ne porte que des tubercules aplatis. Le dactyle est armé dorsalement de dents épineuses, plus aiguës que sur le reste de la main, et, sur son bord préhensile, de deux fortes dents triangulaires non cornées. Sur le carpe, en dehors des dents assez fortes implantées sur la région dorso-mésiale, la face dorsale ne porte que quelques denticules espacés.

Deuxièmes (fig. 9) et troisièmes péréiopodes un peu plus longs à droite qu'à gauche, dépassant largement les chélipèdes. Dactyle toujours nettement plus long que le propode ; celui-ci subcylindrique, la largeur de sa face latérale comprise entre 2,5 (P3 gauche) et 3 fois (P3 droit) dans sa longueur. Bord ventral du mérus denticulé sur toute sa longueur sur les deuxièmes péréiopodes, avec seulement des indentations sétifères sur les troisièmes. Tous les articles dorsalement inermes, à l'exception d'une petite dent dorso-distale et d'une ligne dorsale de dents à pointe cornée sur le carpe des deux paires d'appendices ; ces dents sont petites et peu apparentes sur les troisièmes péréiopodes. Bord ventral du dactyle avec une ligne de 10-12 fines épines cornées noires ; des épines analogues, en nombre variable, sur la face mésiale de cet article, plus nombreuses sur les deuxièmes péréiopodes que sur les troisièmes.

Sur l'abdomen, plaques tergales 2-5 grandes, en contact quand cette partie du corps est en

extension. Sixième tergite divisé par une profonde dépression transverse et par une dépression longitudinale médiane, moins marquée sur la partie antérieure ; celle-ci couverte de petites dépressions et de tubercules aplatis, à pointe cornée orientée vers l'arrière. Bord postérieur de ce tergite inerme (fig. 12).

Telson (fig. 12) modérément asymétrique : le lobe postérieur gauche est saillant, long et large, arrondi au sommet, le lobe droit nettement plus court, mais de forme similaire ; les deux lobes sont séparés par une concavité régulière profonde.

Quatre pléopodes impairs (Pl2 à Pl5) dans les deux sexes, présentant les caractéristiques décrites pour le genre.

Pilosité : Des soies fines, assez longues, en petits faisceaux espacés sur l'écusson et sur la surface calcifiée, en arrière du sillon cervical. Sur les trois premières paires d'appendices thoraciques des soies un peu plus épaisses, la plupart longues, implantées en faisceaux ou en courtes rangées transverses ; ces soies sont plus denses sur les régions dorsales et latérales des articles distaux. Les deux dernières paires thoraciques sont également assez fortement pileuses. De longues soies fines sont présentes sur les tergites abdominaux et sur le telson, formant en particulier des franges marginales.

Coloration (quelques semaines après la fixation) : Écusson blanc grisâtre très légèrement rosé. En vue dorsale, le tiers proximal des pédoncules oculaires d'un rouge orange intense s'éclaircissant vers l'avant et passant au rose uniforme sur la moitié distale. Du côté ventral le rouge s'étend de façon variable vers l'avant, parfois jusqu'au voisinage des cornées. Les écailles oculaires, les deux premiers articles des pédoncules antennulaires et les quatre premiers des pédoncules antennaires d'un rouge intense ; l'article distal de ces pédoncules est rosé, la moitié distale des flagelles antennaires rouge. Les trois premières paires thoraciques blanc jaunâtre, avec le mérus largement teinté de rouge. Les deux dernières paires thoraciques, le sixième tergite abdominal et les uropodes sont uniformément blanc jaunâtre. Les soies sont de teinte fauve, celles des chélipèdes parfois légèrement rosées sur leur moitié proximale.

Remarques

Les dix spécimens d'après lesquels a été décrit *Bathynarius pacificus* ont une coloration tout à fait identique. Ils présentent quelques variations dans les proportions de l'écusson qui, chez les huit mâles, dont les tailles s'échelonnent entre 8,1 et 11 mm, a une longueur le plus souvent nettement supérieure à sa largeur, les trois individus les plus grands ayant un allongement maximum, avec un rapport des dimensions de 1,16 ou 1,17. Chez les deux femelles, de 5 et 6,1 mm, longueur et largeur sont sensiblement égales. Chez tous ces exemplaires, des sillons distincts sont visibles sur la face dorsale de l'écusson : ceux qui forment un Y inversé sur la moitié antérieure peuvent être marqués par de fines lignes décalcifiées ou atténués et peu apparents, alors que ceux qui forment un V aux branches arquées sur la région postérieure sont plus profonds, toujours en grande partie décalcifiés et se prolongent parfois en une ligne médiane jusqu'au sillon cervical.

La longueur des pédoncules oculaires varie quelque peu en fonction de la taille des individus : ils sont relativement plus courts chez les plus grands ; leurs proportions restent cependant à peu près les mêmes, sauf chez les plus petits, les deux femelles, où ils sont

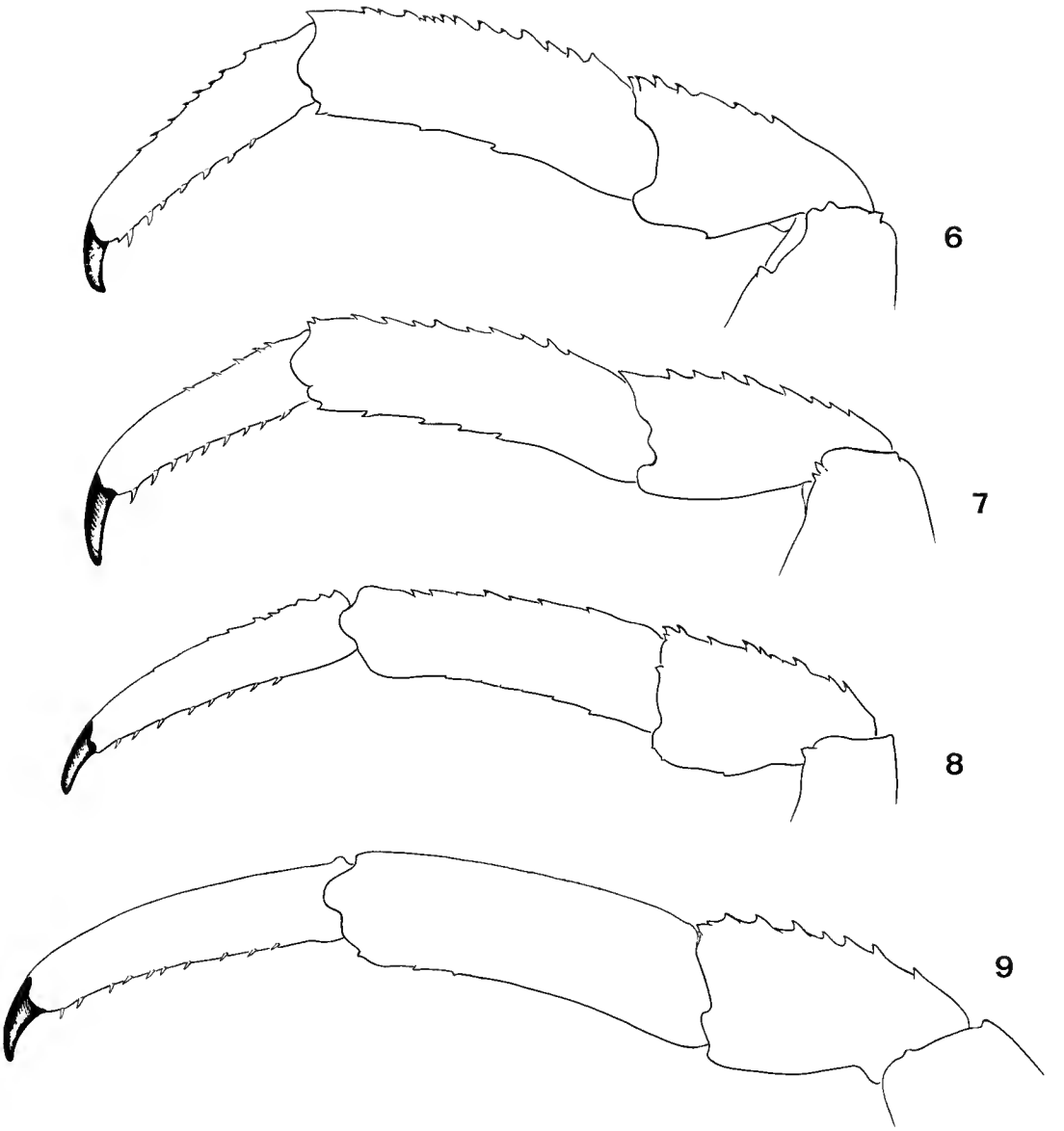

FIG. 6-9. — Carpe, propode et dactyle du 2e péréiopode gauche, vue latérale : 6, *Bathynarius anomalus* (A. Milne Edwards et Bouvier), « Gerda », st. 387 (Floride), femelle 5,2 mm ; 7, *B. albicinctus* (Alcock), SMCB, st. 322 (Tuamotu), femelle 5,4 mm ; 8, *B. wolffi* sp. nov., The Danish Expedition to the Kei Islands 1922, st. 3, mâle holotype 5,7 mm ; 9, *B. pacificus* sp. nov., SMCB, st. 303 (I. Marquises), mâle holotype 10,5 mm (× 10, sauf 9, x 6).

beaucoup moins grêles, avec un indice cornéen de 4,6 chez l'une, de 5,1 chez l'autre, contre 5,7 en moyenne chez les mâles.

Le développement des dents épineuses sur la région dorsale des trois premières paires d'appendices thoraciques semble également lié à la taille. Sur la main des chélipèdes ces dents sont relativement plus courtes et moins nombreuses chez les petits exemplaires. De même, ceux-ci sont moins fortement armés sur le carpe des deuxièmes péréiopodes, la femelle de 5 mm ne portant que quelques denticules localisés sur la région distale de cet article.

D'autres variations sont sans relation avec la taille des individus. Ainsi, les pédoncules des antennules, en extension, peuvent dépasser plus ou moins largement les yeux et ceux des antennes arriver juste à la base des cornées ou presque atteindre leur bord antérieur.

B. pacificus ne semble pas présenter d'affinités particulières avec l'une des trois autres espèces maintenant rangées dans le genre. Il convient cependant de relever les caractères qui le distinguent de *B. albicinctus*, puisque les deux espèces peuvent cohabiter. Elles ne diffèrent pas par les proportions de l'écusson céphalothoracique ni par la forme et l'avancée du rostre qui, chez l'un et chez l'autre, obtus, parfois émoussé au sommet, dépasse de peu les saillies postantennaires. Les sillons de la face dorsale, tels qu'ils ont été décrits chez *B. pacificus*, sont incomplètement représentés chez *B. albicinctus* : ils manquent ou sont à peine discernables sur la région antérieure, alors que sur la région postérieure ils se réduisent le plus souvent à deux faibles sillons arqués, interrompus bien avant d'atteindre la ligne médiane.

Les pédoncules oculaires diffèrent, non par leur longueur qui, chez les deux espèces, est d'un quart à un cinquième inférieure à celle de l'écusson, mais par leurs proportions : l'indice cornéen est en général inférieur à 5 chez *B. albicinctus* et le plus souvent supérieur à 5,5 chez *B. pacificus*.

Les pédoncules antennulaires et antennaires sont plus courts chez *B. albicinctus* : les premiers ne dépassent que de peu la base des cornées et les seconds n'atteignent pas cette base. L'écaille antennaire est également plus courte et armée de denticules épineux plus petits et plus nombreux que chez *B. pacificus*.

En ce qui concerne les chélipèdes, la forme et l'ornementation de la main séparent les deux espèces. Chez l'une et chez l'autre, elle est approximativement deux fois plus longue que large, mais chez *B. pacificus* (fig. 4) les doigts sont relativement plus courts : ils sont à peine plus longs que la paume ; en outre, celle-ci est plus renflée. La face dorsale est couverte de dents coniques à pointe cornée, de taille régulière dans l'ensemble, alors que chez *B. albicinctus* (fig. 2) on observe un petit nombre de dents assez fortes, entre lesquelles s'intercalent de nombreux denticules. La surface latéro-ventrale de la main, revêtue de tubercules ou denticules cornés peu saillants chez l'espèce d'Alcock, ne présente chez *B. pacificus* que des rugosités sétifères.

Les deuxièmes et troisièmes péréiopodes ont toujours un dactyle nettement plus long que le propode chez *B. pacificus*, alors que le premier de ces articles est égal au second ou, souvent, plus court chez *B. albicinctus*. Par ailleurs, ce dernier a des pattes plus grêles : ainsi, la hauteur maximale du propode est comprise environ 3,4 fois dans sa longueur sur les P2 et 3 fois sur les P3, les rapports homologues étant respectivement de 3 et de 2,5 chez *B. pacificus*. L'ornementation est également différente : chez l'espèce nouvelle, les articles des P2 sont dorsalement inermes, à l'exception du carpe qui porte une ligne irrégulière de dents cornées, et du dactyle qui, ventralement, est armé d'un petit nombre d'épines cornées brunes ; sur les P3, seul le carpe est doté d'un denticule distal. Chez *B. albicinctus*, carpe, propode et dactyle des

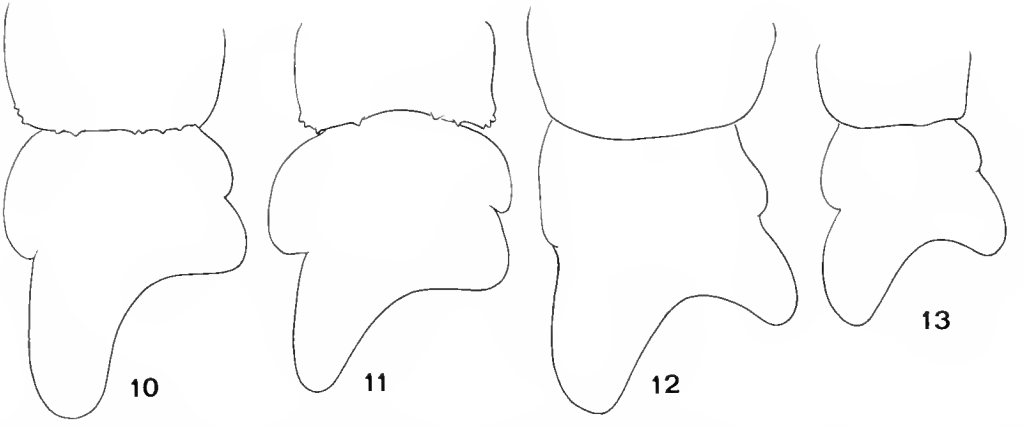

FIG. 10-13. — Bord postérieur du 6e tergite abdominal et telson (× 9) : 10, *Bathynarius albicinctus* (Alcock), SMCB, st. 337 (I. Tubuaï), mâle 7,0 mm ; 11, *B. anomalus* (A. Milne Edwards et Bouvier), « Gerda », st. 251 (Floride), mâle 7,6 mm ; 12, *B. pacificus* sp. nov., SMCB, st. 303 (I. Marquises), mâle paratype 9,5 mm ; 13, *B. wolffi* sp. nov., The Danish Expedition to the Kei Islands 1922, st. 3, mâle holotype 5,7 mm.

deux paires ont une large couverture dorsale de denticules épineux dont le développement est variable, parfois très petits et peu apparents, sur les P3 surtout.

B. pacificus se distingue encore par l'absence de denticulations sur le bord postérieur du sixième tergite abdominal et par le telson moins asymétrique que chez *B. albicinctus* : son lobe gauche est plus court et son lobe droit, non pas très arrondi, mais assez saillant.

La pilosité est assez variable chez les deux espèces, mais offre cependant dans l'ensemble des différences spécifiques : chez *B. pacificus*, les soies sont un peu plus épaisses et, sur les régions dorsales des appendices thoraciques, plus longues, plus égales et plus denses.

En dehors des caractères distinctifs énoncés ci-dessus, *B. pacificus* et *B. albicinctus* présentent chacun une coloration particulière, persistant longtemps dans l'alcool et qui permet leur reconnaissance immédiate. Le premier a des appendices thoraciques d'un blanc jaunâtre uniforme et des pédoncules oculaires fortement pigmentés sur leur tiers proximal au moins. Chez le second les pattes sont d'un rouge vermillon intense largement annelé de blanc, le rouge étant constellé de taches et points blancs marquant les implantations de soies ; les pédoncules oculaires sont blancs sur toute leur longueur.

Bathynarius wolffi sp. nov.

(Fig. 5, 8, 13, 14)

MATÉRIEL EXAMINÉ. — **Iles Kei**, The Danish Expedition to the Kei Islands 1922, station 3, 30.03.1922, 5°32 S, 132°36'E, 245 m, sable : 1 ♂ 5,7 mm (Zoologishe Museum, Copenhague).

TYPE ET LOCALITÉ-TYPE. — Voir ci-dessus.

COQUILLE. — *Cymatium* sp.

DESCRIPTION

Écusson céphalothoracique (fig. 14) légèrement plus long que large. Bords latéraux régulièrement convexes, avec une indentation en arrière de leur milieu. Rostre en triangle obtus, à sommet émoussé dépassant les saillies postantennaires qui sont arrondies et inermes. Écusson creusé de dépressions bien marquées donnant à la surface un aspect corrodé, sauf dans la partie centrale de la région gastrique qui est simplement ponctuée. En arrière du rostre, une courte gouttière longitudinale avec une fine ligne axiale décalcifiée. Pas de sillon transverse sur la partie antérieure de la région cardiaque.

Pédoncules oculaires égaux, très faiblement renflés à la base, leur longueur sensiblement égale aux trois quarts de celle de l'écusson. Cornées grandes, un peu plus longues que larges ; leur diamètre compris 4,5 fois environ dans la longueur des pédoncules. Écailles oculaires largement espacées, courtes, leur sommet brièvement bidenté.

Pédoncules antennulaires dépassant quelque peu les yeux.

Pédoncules antennaires atteignant juste la base des cornées. Deuxième article à angle antéro-latéral non saillant, arrondi, à gauche, formant une courte saillie à sommet arrondi, inerme, à droite. Écaille antennaire atteignant le tiers proximal du dernier article ; elle est triangulaire, forte, mais faiblement armée : en arrière de son sommet peu aigu, une dent courte, émoussée, et une dent latérale submédiane qui, à droite, est très petite, à peine discernable. Flagelle un peu plus long que la carapace.

Chélipèdes semblables, le gauche un peu plus grand que le droit. Une large fissure longitudinale membraneuse sur la face ventrale de la coxa. Faces latérale et mésiale du mérus très faiblement convexes, avec des tubercules arrondis sur la moitié distale de leurs bords ventraux ; ces faces ont une largeur maximale égale aux trois cinquièmes environ de la longueur de l'article. Main (fig. 5) à paume renflée du côté ventral, le rapport de sa longueur à sa largeur maximale légèrement inférieur à 2. Doigts un peu plus longs que la paume. Face dorsale recouverte de dents coniques à pointe cornée ; ces dents sont fortes, assez rapprochées près du bord latéral, où elles tendent à former deux lignes qui s'étendent sur le doigt fixe et dont la plus latérale compte une dizaine de dents ; elles sont également assez rapprochées près du bord mésial, mais sont peu nombreuses et espacées sur la région médiane. Le doigt fixe est armé dorsalement d'épines cornées courtes et larges, quelque peu aplaties ; son bord préhensile porte des dents molariformes dont l'une, grosse, massive, s'avance quelque peu au-dessus de la base de l'ongle. La face latérale de la paume, nettement séparée de la face dorsale, est presque plane, inerme, mais avec des ponctuations sétifères ; des épines cornées courtes, fortes, réapparaissent sur la face ventrale. Le dactyle porte des dents cornées plus petites que sur le propode, mais avec un sommet corné élargi et aplati ; son bord préhensile est armé de deux grosses dents principales et un processus proximal triangulaire s'avance au-dessus de la base du doigt fixe.

Deuxièmes (fig. 8) et troisièmes péréiopodes plus longs à droite qu'à gauche, dépassant largement les chélipèdes. Dactyle légèrement plus long que le propode, ce dernier article subcylindrique, sa hauteur maximale comprise 3,2 fois dans sa longueur, sauf sur la P3 gauche dont le propode, plus court, n'est que 2,7 fois plus long que haut. Bord ventral du mérus denticulé sur toute sa longueur sur les P2, avec seulement des indentations sétifères sur les P3. Sur les P2, dorsalement, le carpe est armé d'une ligne de dents à pointe cornée aiguë, fortement inclinées vers l'avant ; le propode porte sur toute sa surface dorsale des denticules cornés

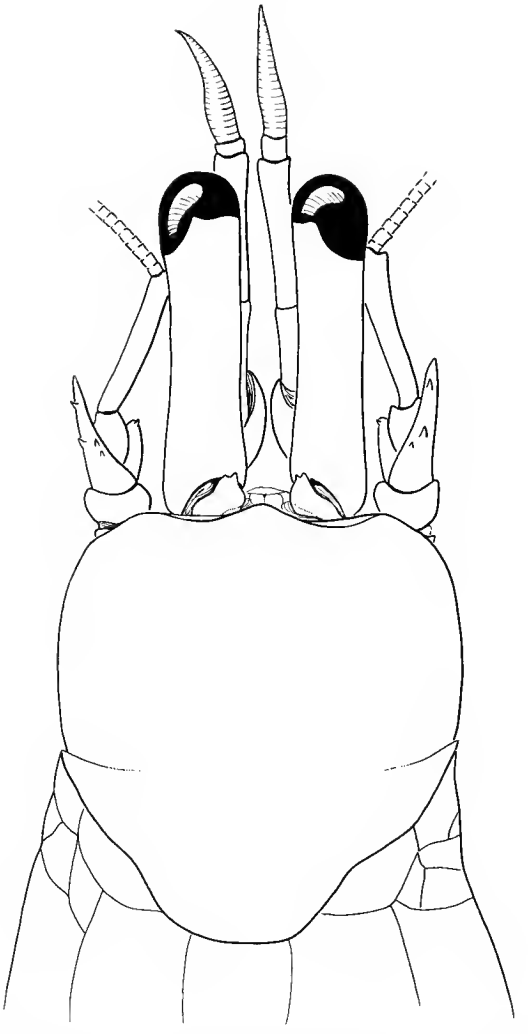

FIG. 14. — *Bathynarius wolffi* sp. nov., The Danish Expedition to the Kei Islands 1922, st. 3, mâle holotype 5,7 mm : Région antérieure de la carapace et appendices sensoriels (× 10).

arrangés en deux lignes irrégulières et des denticules similaires sont présents sur le dactyle. Les P3 sont plus faiblement épineux, avec un seul denticule, distal, sur le carpe, et des denticules ou spinules sur le propode et le dactyle, moins nombreux que sur les P2. On observe sur le dactyle des deux paires une ligne ventrale de 8-10 épines cornées et des spinules sur sa face mésiale.

Sur l'abdomen, plaques tergales 2-5 grandes, très rapprochées. Sixième tergite divisé par une profonde dépression transverse ; un fin sillon longitudinal médian sur la partie antérieure,

se prolongeant sur la partie postérieure par une large dépression ; la partie antérieure est uniformément couverte de minuscules denticules épineux. Bord postérieur de ce tergite inerme (fig. 13).

Telson (fig. 13) avec les deux lobes postérieurs saillants, le gauche large à la base, très arrondi au sommet, le droit plus court mais de forme similaire ; les deux lobes sont séparés par une concavité régulière assez profonde.

Quatre pléopodes impairs, le premier légèrement plus petit que les suivants. Sur tous l'exopodite est bien développé, l'endopodite présent, mais rudimentaire.

Pilosité : Région antérieure du corps et appendices sensoriels faiblement pileux : quelques fines soies fasciculées sur l'écusson et des soies un peu plus longues sur l'écaille antennaire. Sur la face dorsale des chélipèdes, des soies de longueur variable disposées en éventail à la base des dents à pointe cornée : ces soies, assez longues sur le carpe, ont une taille décroissante à partir de la base de la main. La région dorsale des appendices thoraciques suivants est également revêtue de soies assez longues mais peu denses.

Coloration : L'holotype, seul spécimen connu, recueilli en 1922, est décoloré. Les téguments calcifiés sont dans l'ensemble d'un blanc crémeux avec des reflets irisés. Cependant on discerne sur le dactyle des pattes ambulatoires une très légère teinte rosée, avec deux anneaux blancs, l'un proximal, l'autre distal.

Remarques

Bathynarius wolffi sp. nov. est décrit d'après un unique spécimen recueilli par Th. Mortensen au large des îles Kei. La nouvelle espèce répond à la diagnose et à la définition du genre, telles qu'elles ont été proposées lors de son établissement, sauf sur deux points : il n'y a pas trace de sillon transverse sur la région cardiaque et le bord postérieur du sixième tergite abdominal est inerme, comme chez *B. pacificus* sp. nov.

Certaines des différences qui séparent *B. wolffi* des deux autres *Bathynarius* indo-ouest pacifiques sont minimes et devront être confirmées par l'examen d'un matériel supplémentaire, mais d'autres sont très nettes et ne laissent place à aucune confusion.

Compte tenu des variations de *B. albicinctus* et de *B. pacificus* en fonction de la taille, le type de *B. wolffi*, a été plus particulièrement comparé à des spécimens de dimensions voisines.

On ne relève pas de différences significatives dans la forme ni dans les proportions de l'écusson, mais sa surface ne présente pas trace des lignes ou sillons sur la région gastrique, toujours bien apparents chez *B. pacificus*, atténués et incomplets chez *B. albicinctus*. La longueur des pédoncules oculaires rapportée à celle de l'écusson et leurs proportions sont assez voisines chez les trois espèces. On note cependant que ces pédoncules sont légèrement plus robustes et les cornées un peu plus grandes chez *B. wolffi*. Chez celui-ci, les écailles oculaires sont, non pas unidentées, mais brièvement bidentées, et la saillie antéro-latérale du deuxième article des pédoncules antennaires n'est pas triangulaire et denticulée, mais courte, arrondie et inerme.

Les trois premières paires de péréiopodes se rapprochent de ceux de *B. pacificus* par les proportions de leurs articles, avec des différences minimes dont la signification est douteuse, s'agissant d'un seul individu. Par contre, leur ornementation constitue l'un des caractères qui

distinguent le plus nettement *B. wolffi* des autres *Bathynarius*. Ce caractère sépare sans ambiguïté *B. albicinctus* de *B. pacificus* (supra, p. 492). Or, les dents, denticules et épines sur ces appendices offrent encore un développement et un arrangement autres chez *B. wolffi*. Sur les chélipèdes, la face dorsale de la paume (fig. 5) rappelle celle de *B. pacificus* dans la mesure où elle porte des dents coniques à pointe cornée, de dimensions assez homogènes ; cependant ces dents sont plus grandes et moins nombreuses chez le type de *B. wolffi* que chez des individus de taille voisine appartenant à l'autre espèce. De plus, chez ceux-ci le doigt fixe est armé de dents semblables à celles de la paume, quoique plus petites, c'est-à-dire qu'elles sont dressées et ont une forte base conique calcifiée surmontée d'une petite pointe cornée ; chez *B. wolffi*, la partie cornée est plus développée par rapport à la base, élargie en triangle ou arrondie, et plus ou moins aplatie. Les deux paires thoraciques suivantes sont plus épineuses chez *B. wolffi*, avec des dents ou denticules cornés sur le carpe, le propode et le dactyle des P2, et des denticules sur le propode et le dactyle des P3, alors que chez *B. pacificus* seul le carpe des P2 est armé.

Le bord postérieur du sixième tergite abdominal est inerme, comme chez *B. pacificus*, alors qu'il est denticulé chez *B. albicinctus*. Le telson des deux espèces nouvelles diffère quelque peu dans son contour mais chez l'une et chez l'autre le lobe droit est assez saillant, alors qu'il est très court et arrondi chez *B. albicinctus*.

La pilosité, telle que ce caractère, assez variable, apparaît sur le type, serait plus faible que chez *B. pacificus* : les soies sont dans l'ensemble moins longues et moins denses et, sur la main des chélipèdes, leur taille diminue rapidement à partir de la base.

Le spécimen décrit est presque complètement décoloré. Cependant, la très légère teinte rosée visible sur une partie du dactyle des pattes ambulatoires laisserait supposer que, sur le vivant, cet article est rouge et annelé de blanc à ses extrémités, comme chez *B. albicinctus*. Ceci ne permet évidemment pas de préjuger du reste de la coloration.

Remarques complémentaires sur les caractères et la distribution du genre *Bathynarius*

L'introduction de deux espèces supplémentaires dans un genre établi avec deux espèces incluses conduit nécessairement à contrôler sa définition et sa diagnose. En fait, celles-ci se sont trouvées en grande partie confirmées : les deux taxa nouveaux présentent, outre un habitus similaire, la plupart des caractères auxquels avait été accordée une signification générique. C'est le cas, entre autres, de la forme de l'écusson et du rostre, du grand développement des tergites de l'abdomen, de la forte asymétrie du telson, du large écartement des pédoncules oculaires, et de la structure et de l'ornementation des chélipèdes, avec l'existence d'une fissure longitudinale membraneuse sur la face ventrale de la coxa et la couverture épineuse du carpe et de la main. Les pièces buccales, décrites et figurées chez *B. anomalus* (Forest, 1989: 762, fig. 5 b, d, g, j, k) n'offrent que des différences spécifiques minimes dans les proportions et la spinulation de certains articles : ainsi, chez *B. pacificus*, le bord ventral du mérus des 3e maxilipèdes est armé de 2, rarement 3, dents assez aiguës , au lieu de 4-5, obtuses , chez *B. anomalus*. De même, la disposition et la structure des quatre pléopodes impairs sont sensiblement les mêmes : ces appendices sont presque égaux et le quatrième a, chez les femelles, la même fonction ovifère que les précédents.

La définition précédemment établie nécessite cependant quelques amendements. Le plus important, à apporter également à la diagnose, concerne le sillon transverse sur la région cardiaque : présent chez tous les *B. pacificus* examinés, il manque totalement chez le type et unique spécimen connu de *B. wolffi*. Deux autres points appellent des corrections d'ordre mineur : l'un est relatif à la conformation des écailles oculaires, l'autre à celle du bord postérieur du sixième tergite abdominal. Dans la définition du genre, les écailles oculaires ont été notées comme unidentées. Or, chez le type de *B. wolffi*, elles sont brièvement bidentées ; ceci peut cependant résulter d'une anomalie, d'autant plus que, chez certains *B. pacificus*, leur sommet peut être tronqué d'un côté ou de l'autre et surmonté de deux denticules plus ou moins distincts. Quant au sixième tergite abdominal, son bord postérieur est inerme chez les deux espèces décrites ici, alors qu'il est denticulé chez *B. anomalus* et chez *B. albicinctus*.

Trois des espèces rangées dans le genre *Bathynarius* sont connues par un nombre d'exemplaires suffisant pour qu'elles aient pu être comparées de façon significative, en tenant compte de leur variabilité. La quatrième, bien que représentée par un spécimen unique, est aussi incontestablement distincte. S'il est maintenant possible de confirmer que *B. anomalus* diffère de *B. albicinctus*, non seulement par la coloration, mais par une série de traits morphologiques, on constate également que les trois espèces indo-ouest pacifiques ne présentent pas d'affinités particulières qui les opposeraient à celle de l'Atlantique occidental. Au contraire, par certains caractères — ornementation des chélipèdes et des deux paires de pattes thoraciques suivantes, proportions des articles de ces dernières — les deux espèces nouvelles apparaissent comme plus proches de *B. anomalus* que de *B. albicinctus*.

Présentant des différences spécifiques nettes mais de peu d'ampleur, les *Bathynarius* vivent dans des conditions écologiques assez voisines. Tous ont été recueillis dans des régions où existent des formations coralliennes et à des profondeurs comparables. Les échantillons de *B. anomalus*, de loin les plus nombreux dans le matériel examiné, provenaient d'une quarantaine de stations s'échelonnant de 100 à plus de 400 m de profondeur, mais la plupart entre 200 et 300 m, alors que les trois autres espèces ont surtout été capturées entre 250 et 300 m.

La distribution géographique des *Bathynarius* (fig. 15) apparaît aujourd'hui, nous l'avons dit, comme considérablement plus étendue qu'au moment où le genre a été créé. A l'Atlantique occidental, où *B. anomalus* semble commun au large des Petites et Grandes Antilles, et à l'océan Indien (sud de l'Inde et île de La Réunion) s'ajoutent l'Indonésie et la Polynésie. Cette extension ne va pas à l'encontre de l'hypothèse d'une origine thétysienne pour le genre et, à cet égard, rapproche celui-ci des *Pylocheles* (FOREST, 1989 : 783).

L'homogénéité morphologique du genre *Bathynarius* et les similitudes qu'offrent ses représentants dans leur écologie semblent donc aller de pair avec une très large distribution à travers les océans. Ceci est également observé chez d'autres Diogenidae, à la fois peu diversifiés dans leur morphologie, vivant dans des conditions écologiques relativement uniformes, en particulier en ce qui concerne la profondeur, et présentant en même temps une vaste aire de dispersion. C'est le cas des *Clibanarius*, dont les nombreuses espèces ne se distinguent guère, souvent, que par la coloration : toutes habitent essentiellement la zone intertidale ou son voisinage immédiat et sont communes dans les mers tropicales et subtropicales. De même, les trois espèces du genre *Petrochirus*, morphologiquement assez voisines, vivent dans des limites de profondeurs relativement étroites, surtout entre 30 et 50 m, de part et d'autre de l'Atlantique et dans le Pacifique oriental. Au contraire, d'autres genres à grande extension géogra-

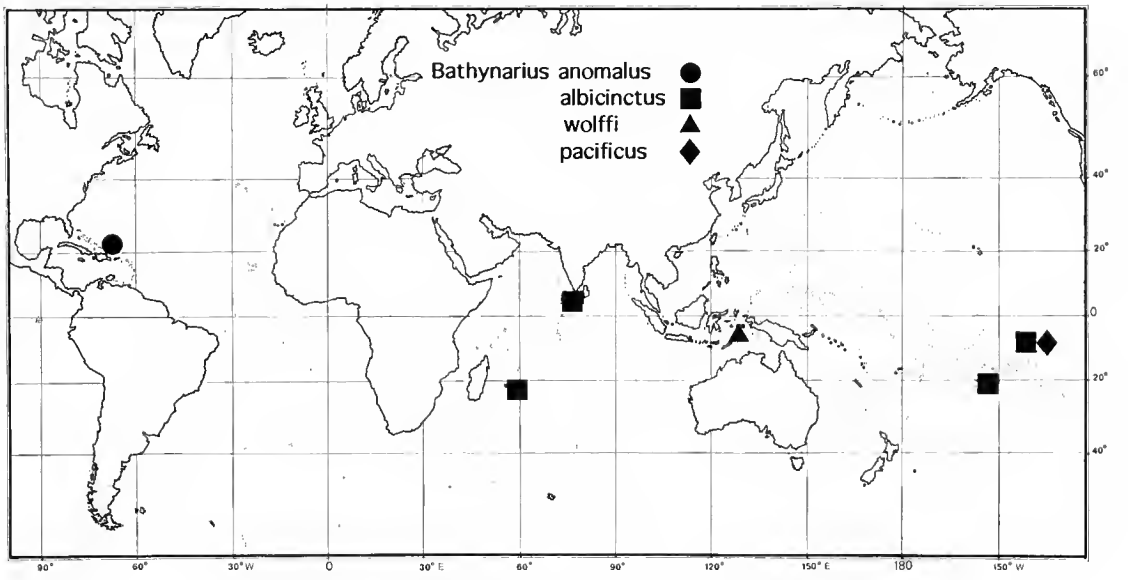

FIG. 15. — Distribution géographique du genre *Bathynarius*.

phique, tels *Diogenes, Dardanus* et *Paguristes*, présentent une forte diversification spécifique en partie liée à des adaptations à des niveaux bathymétriques et à des conditions écologiques différents.

CLEF D'IDENTIFICATION DES ESPÈCES DU GENRE *Bathynarius*

1. Bord postérieur du 6e tergite abdominal irrégulièrement denticulé. Lobe droit du telson très arrondi, saillant du côté latéral, mais non ou à peine du côté postérieur 2

— Bord postérieur du 6e tergite abdominal inerme. Lobe droit du telson ovalo-triangulaire, notablement saillant du côté postérieur 3

2. Main des chélipèdes recouverte de dents coniques fortes, de taille relativement uniforme. Coloration d'ensemble rose saumon clair, fugace. — Grandes et Petites Antilles ..... *anomalus*

— Main des chélipèdes recouverte de dents de taille irrégulière, certaines assez fortes parmi de nombreux denticules. Coloration vive persistante : les appendices thoraciques d'un rouge intense ponctué de blanc, et cerclés de blanc. — Inde, La Réunion, îles Marquises et Tubuai ..... *albicinctus*

3. Un sillon transverse sur la région cardiaque. Bord dorsal du propode des 2e péréiopodes inerme. — Iles Marquises ..... *pacificus*

— Pas de sillon transverse sur la région cardiaque. Bord dorsal du propode des 2e péréiopodes denticulé. — Iles Kei ..... *wolffi*

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Deepwater Xanthid crabs from French Polynesia (Crustacea, Decapoda, Xanthoidea)

by Peter J. F. Davie

Abstract. — A collection of brachyuran crabs of the family Xanthidae, trapped in deepwater in French Polynesia, has been studied. Of a total of 13 species, 10 are described as new, and four new genera are erected : *Alainodaeus* gen. nov. to include *A. akiaki* sp. nov. and *A. rimatara* sp. nov. ; *Epistocavea* gen. nov. to include *E. mururoa* sp. nov. ; *Meriola* gen. nov. to include *M. rufomaculata* sp. nov. ; and *Rata* gen. nov. to include *R. tuamotense* sp. nov. Five species are described in existing genera : *Banareia fatuhiva* sp. nov. ; *Euryozius danielae* sp. nov. ; *Medaeus grandis* sp. nov. ; *Meractaea tafai* sp. nov. ; and *Paraxanthodes polynesiensis* sp. nov. The records of *Demania garthi* Guinot and Richer de Forges, 1981, *Demania mortenseni* (Odhner, 1925), and *Lophozozymus bertonciniae* Guinot and Richer de Forges, 1981, all represent considerable eastwardly range extensions. *Actaea mortenseni* Odhner, 1925, removed from *Actaea* by Guinot (1976) and subsequently *incertae sedis* is re-described and placed into *Demania* for the first time.

Résumé. — Une collection de crabes de la famille des Xanthidae, capturés en eau profonde, en Polynésie française, au moyen de casiers, est étudiée. Sur un total de 13 espèces, 10 sont nouvelles pour la Science. Quatre genres nouveaux sont créés : *Alainodaeus* pour recevoir *A. akiaki* sp. nov. et *A. rimatara* sp. nov. ; *Epistocavea* pour *E. mururoa* sp. nov. ; *Meriola* pour *M. rufomaculata* sp. nov. ; *Rata* pour *R. tuamotense* sp. nov. Cinq des espèces nouvelles appartiennent à des genres déjà décrits : *Banareia fatuhiva*, *Euryozius danielae*, *Medaeus grandis*, *Meractaea tafai* et *Paraxanthodes polynesiensis*. *Demania garthi* Guinot and Richer de Forges, 1981, *D. mortenseni* (Odhner, 1925) et *Lophozozymus bertonciniae* Guinot and Richer de Forges, 1981, sont signalées pour la première fois en Polynésie française, ce qui étend considérablement, vers l'est, leur aire de distribution. *Actaea mortenseni* Odhner, 1925, exclue du genre *Actaea* par Guinot (1976) et devenue ainsi un *incertae sedis*, est redécrite et placée, pour la première fois, dans le genre *Demania*.

Key words. — Crustacea, Brachyura, Xanthidae, deepwater fauna, trapping, Pacific Ocean, French Polynesia.

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Introduction

The last 20 years have considerably improved our knowledge of the crab fauna of the western Pacific Ocean. The MUSORSTOM I, II and III Expeditions, under the direction of Professor Jacques Forest, in 1976, 1980 and 1985, have led to important studies of the bathyal fauna of the Philippines (Forest, 1981, 1986 ; Serène and Vadon, 1981). The investigation of the bathyal zone of the plateau of the Chesterfield Islands and of New Caledonia has been

undertaken with several cruises *viz.* CHALCAL I and II, BIOCAL, MUSORSTOM IV and V (see RICHER DE FORGES, 1990), and the results of the study of some of the collected material, in particular the Crustacea, has been published as part of the French MUSORSTOM Series.

Along the Australian coast, the deepwater crustacean fauna has been systematically investigated recently by the cruises of CIDARIS I, II, and III, and collections made by R.V. 'Soela'. Papers on crabs by the following authors are beginning to fill the gaps in our knowledge of this poorly known region (GRIFFIN and BROWN, 1976 ; GRIFFIN and TRANTER, 1986 *a, b* ; DAVIE and SHORT, 1989 ; and DAVIE and RICHER DE FORGES (in prep.).

The present study is based on a part of the crab collections made by J. POUPIN of the French Service Mixte de Contrôle Biologique (SMCB). The collections were made from the F.R.V. 'Marara' which has been carrying out a biological survey throughout French Polynesia. Among the fishing activities, traps are set on the outer slopes of the islands in depths ranging from 100 to 1000m. The details of the gear operations and the yields of Pandalidae shrimps are given in POUPIN *et al.* (1990). POUPIN and RICHER DE FORGES (1991) have briefly outlined the study and their report stresses " the richness and high degree of endemicity of this poorly known area ". Photographs taken on board vessel by J. POUPIN have allowed the life colours of several of the species to be described.

The deepwater of the central and southern Pacific Ocean is still a treasure-house of new taxa. GUINOT and RICHER DE FORGES (1981*a, b*) described three new genera and twelve new species of crabs from deepwater in the Indo-Pacific Region, and notably, ten of these species and two of the genera are only represented in the Pacific. Of the present collection of 13 species from just one family, the Xanthidae, 10 are new to science, and four new genera are needed to accommodate them. Of the remaining three species, two had only been described in the aforementioned work of GUINOT and RICHER DE FORGES (1981*a, b*), and only one was known prior to the 1980s. An additional new species of xanthid crab, *Hypocolpus mararae* Crosnier, 1991, was also collected along with the present specimens, but has been reported on separately by Alain CROSNIER.

Abbreviations used in the text are : AM, Australian Museum, Sydney ; MNHN, Muséum national d'Histoire naturelle, Paris ; QM, Queensland Museum, Brisbane ; USNM, Smithsonian Institution, United States National Museum, Washington. The descriptions for this paper were prepared using the DELTA computer system for generating taxonomic descriptions (DALLWITZ and PAINE, 1986).

The abbreviated terminology used for carapace regions is that used by SERÈNE (1984) following DANA (1852). Measurements given in the text are of carapace breadth (measured at the widest point including lateral spines) followed by length. Leg segments were measured along the top margin and so these were not always the maximum possible length, and this should be borne in mind when using the ratios. The exact limits of the width of the hind margin are also sometimes difficult to determine and in this work they were defined by the point at which the lateral carapace suture meets the rear margin.

List of species of Xanthidae trapped in deepwater in French Polynesia

(* denotes a previous record ; the species is not further discussed in this paper).

Trichiinae De Haan, 1841
Banareia fatuhiva sp. nov.

Xanthinae MacLeay, 1838
Demania garthi Guinot and Richer de Forges, 1981
Demania mortenseni (Odhner, 1925) comb. nov.
Paraxanthodes polynesiensis sp. nov.

Euxanthinae Alcock, 1898
Alainodaeus akiaki gen. nov., sp. nov.
Alainodaeus rimatara gen. nov., sp. nov.
Epistocavea mururoa gen. nov., sp. nov.
* *Hypocolpus mararae* Crosnier, 1991
Medaeus grandis sp. nov.

Actaeinae Alcock, 1898
Meractaea tafai sp. nov.
Rata tuamotense gen. nov., sp. nov.

Zosiminae Alcock, 1898
Lophozozymus bertonciniae Guinot and Richer de Forges, 1981

Liomerinae Sakai, 1976
Meriola rufomaculata gen. nov., sp. nov.

Incertae sedis
Euryozius danielae sp. nov.

Family Xanthidae MacLeay, 1838

Trichiinae De Haan, 1841

Banareia fatuhiva sp. nov.

(Fig. 1 ; pl. 1)

Etymology. — The name refers to the Island of Fatu Hiva, in the Marquises Islands, near where the paratypes were collected. It is treated here as a noun in apposition.

Type material. — The large male (MNHN-B22228) is designated as holotype. The other two specimens are paratypes.

Material examined. — **French Polynesia**. SMCB (J. Poupin) : **Marquises Islands** : Tahuata, Stn 300, 9°54.5′S, 139°07.9′W, trapped 190 m, 1.9.1990 : 1 ♂ 40.4 × 29.9 mm (MNHN-B22228). Fatu Hiva, Stn 306, 10°31.1′S, 138°39.4′W, trapped, 250 m, 4.09.1990 : 1 ♂ 27.4 × 20.5 ; 1 ♀ 27.7 × 20.7 mm (MNHN-B22229).

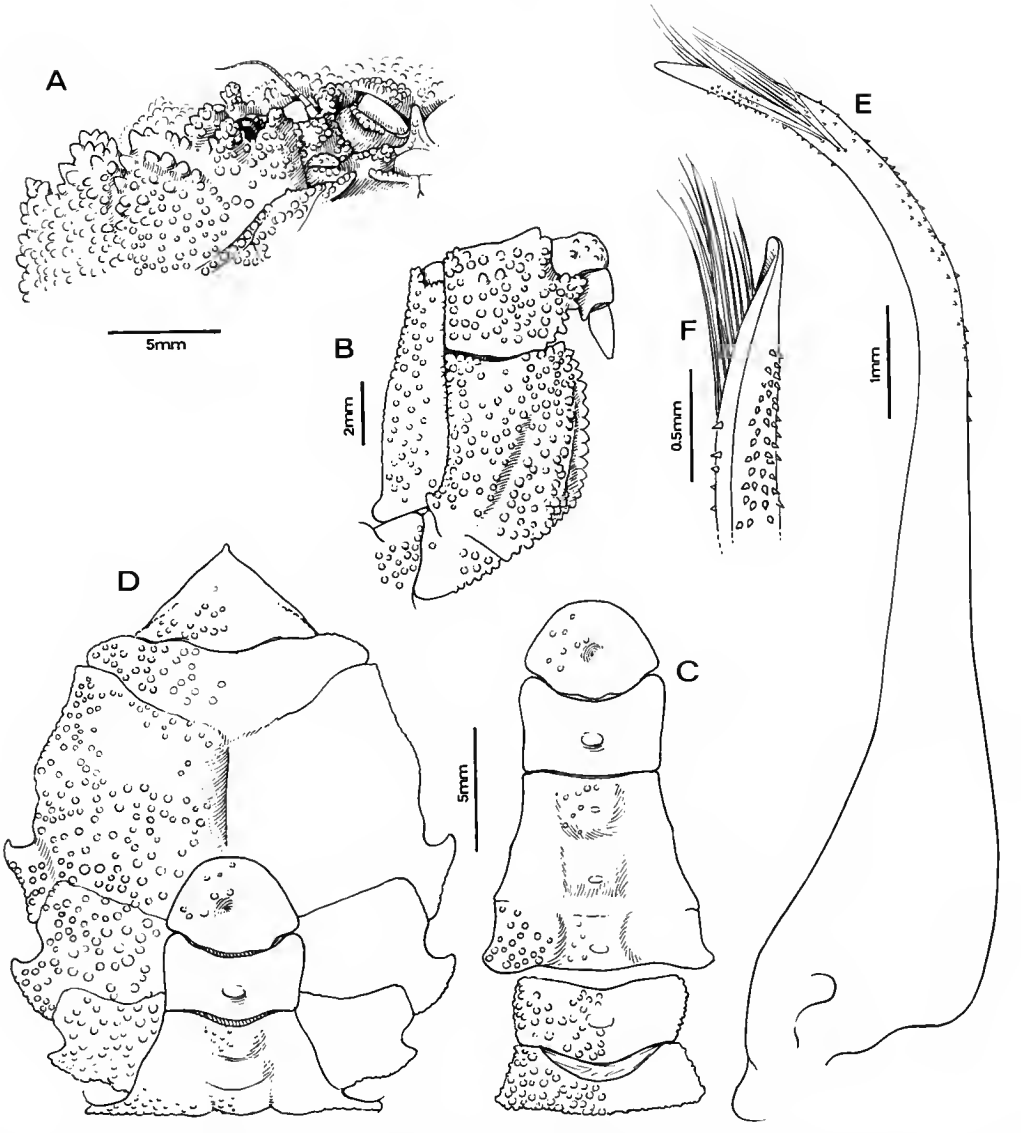

FIG. 1. — *Banareia fatuhiva* sp. nov. Holotype ♂, MNHN-B22228, Tahuata, Marquises Islands. A, frontal view ; B, third maxilliped ; C, abdomen ; D, sternum and abdomen ; E, F, first gonopod.

DESCRIPTION

Carapace sub-globose *c.* 1.34-1.35 times broader than long. Fronto-orbital width *c.* 0.59-0.65 times carapace length. Carapace convex in both directions, but more flattened posteriorly. Regions moderately defined, separated by deep, smooth, narrow grooves ; 1F, 2F and 1M fused ; 1M narrowly obliquely divided from 2M for most of length but connected at

inner posterior corner ; 2M completely separated from 3M ; 2M entire, not subdivided ; 3M with anterior projection very long reaching anteriorly to level with posterior-most point of orbit ; 4M more-or-less clearly separated from 3M ; strong grooves posterior to raised orbital rim ; 2L wide, clearly separated, with raised granular tubercle in anterolateral corner ; lateral regions swollen ; regions behind 2L not strongly demarcated, a narrow groove separating 4L distinct in places, 6L more-or-less well separated ; cardiac region (1P) strongly indicated. Anterolateral margins regularly convex ; granulated ; with four teeth behind the exorbital angle, not strongly projecting ; first tooth an irregularly granular lobe, with posterior granules slightly more prominent ; second and third teeth similar, in the form of granular tubercles ; between teeth 1 and 2, and 2 and 3, are deep, smooth, narrow grooves which continue onto the pterygostome, and meet ventrally so as to describe a triangle ; behind third tooth margin very long, *c.* half total length of anterolateral margin, armed with several strong granules, terminating in a larger granular tubercle at junction with posterolateral margin ; posterolateral margin oblique, slightly concave, rounded. Front *c.* 0.21-0.24 times carapace width ; *c.* 0.49-0.5 times fronto-orbital width ; moderately projecting ; strongly bilobed, with very deep U-shaped sulcus, each tooth roundly triangular ; lateral angles also bluntly acute, strongly separated from medial teeth, but not as strongly projecting. Posterior margin *c.* 0.27-0.3 times carapace width. Carapace surface with granules covering entire surface except for grooves ; granules discrete, on average smaller medially, and larger towards anterolateral margins. Setae of medium length, soft, covering entire surface and give a shaggy appearance. Upper orbital border evenly granular, raised, with strongly projecting tubercular tooth medial to exorbital tooth, separated by smooth narrow grooves ; exorbital tooth granular, also separated by deep narrow grooves. Lower orbital border granular ; armed with two similar, large granular teeth ; sub-orbital and sub-hepatic regions granular, granules becoming coarser dorsally. Antennal flagellum small and entering orbit, reaching just beyond lateral edge of orbit. Basal antennal segment just touching front ; armed distally with small, forwardly projecting, bluntly granular lobe. Antennules folding obliquely ; epistome relatively narrow from side to side, deeply excavated, upper lateral margins with a blunt, granular, medial tooth. Inter-antennular septum narrow.

Third maxilliped : merus distinctly shorter than ischium ; merus wider than long, length *c.* 0.9 times breadth ; inner distal angle below palp produced as sharply granular tooth ; *c.* 0.6 times length of ischium. Ischium rectangular, length *c.* 1.4 times breadth ; inner margin serrated.

Chelipeds subequal ; large and robust. Merus with posterior border granulate ; with broad sub-distal lobe ; lower border granulate ; anterior border sparsely granulate, rounded. Carpus with inner angle not produced, but strongly angular ; inner margin granular ; upper surface and outer margin granular like carapace ; granules present on inner face of carpus just below inner angle. Outer surface of palm entirely covered by thick setae (like carapace) except for distal halves of fingers ; coarsely granular, largest granules arranged in 2-3 more-or-less distinct rows. Inner surface of palm smooth and punctate distally, but with vertical band of large rounded granules proximally. Immovable finger moderately long, with a medial sulcus over proximal two-thirds defined by coarsely granular ridges ; cutting margins bluntly cristate ; fixed finger with 2-3 low teeth in proximal half ; dactyl also with 2-3 proximal teeth but very poorly defined. Length of cutting margin of fixed finger *c.* 0.35 times length propodus. Ventral border of chela concave at base of fixed finger. Dorsal surface of dactyl granular. Fingers pointed ; without a noticeable gape between the cutting margins ; black colouring of fixed finger

continuing onto palm to about two-thirds of distance along ventral margin, proximal edge of colouring oblique on outer face, but more nearly vertical on inner face.

Walking legs : relatively short ; compressed ; broad ; first pair slightly the longest, *c.* 1-1.1 times maximum carapace width. Merus of third leg *c.* 2.2 times as long as wide. Carpus *c.* 1.6 times as long as wide. Propodus *c.* 1.1 times as long as wide. Dactyli longer than propodi ; slender and straight ; terminating in an acute chitinous tip. Merus anterior margin unarmed terminally. Carpus with longitudinal sulcus on upper surface. All segments granular ; thickly covered with soft setae, giving a shaggy appearance.

Male abdomen : third to fifth fused ; third segment slightly the widest. First segment *c.* 0.9 times width third segment. Segments three-five tapering, lateral margin of segment 3 slightly concave. Segment six *c.* 1.8 times wider than long. Telson *c.* 0.8 times longer than wide ; evenly rounded.

Gonopods : G1 long ; slender ; curved ; evenly tapering to pointed tip ; row of long setae present apically on dorsal margin. G2 short ; evenly curved ; tip short.

Sternum : relatively narrow ; granular ; deeply cleft medially on segment 4 ; fused suture line between segments 3 and 4 evident across whole width ; almost entire ventral surface covered with thick shaggy setae like dorsal surface.

Remarks. — The combination of an entire 3M (not tripartite), the undivided 2M, and the relatively poorly lobulated anterolateral margins, separates *Banareia fatuhiva* sp. nov. from all described species except for *B. banareias* (Rathbun, 1911) and *B. villosa* Rathbun, 1906. *B. fatuhiva* is clearly distinguishable from those species by having much more sharply defined regions ; by having the grooves between the first two anterolateral teeth continuing onto the subhepatic region ; by the very long border between the third and fourth anterolateral teeth ; by the very long narrow median lobe of 3M ; and by the distinctive, very prominent, narrow frontal lobes.

Distribution. — Known only from the Marquises Islands, French Polynesia. Bathymetric range : 190-250 m.

Xanthinae MacLeay, 1838

Demania garthi Guinot and Richer de Forges, 1981
(Fig. 2 ; pl. 2)

Demania garthi Guinot and Richer de Forges, 1981*a* : 1121-22, pl. I, 2, 2a

Material examined. — **French Polynesia**. SMCB (J. Poupin) : **Society Islands** : Tubuai, Isles Sous le Vent, Stn 417, 16°14.5′S, 151°47.1′E, trapped, 245 m, 13.5.1991 : 2 ♂ 38.6 × 26.7, 49.6 × 33.8 mm (MNHN). — **Tuamotu Archipelago** : Nihuru, 16°42.8′S, 142°52.8′W, trapped, 220 m, 15.11.1989 : 1 ♀ 45.7 × 31.6 mm (MNHN). Mururoa, 21°46.9′S, 138°55.4′W, trapped, 210 m, 30.11.1989 : 1 ♂ 53.4 × 37.1 ; 1 ♀ 51.0 × 36.0 mm (MNHN). Mururoa, 21°48.1′S, 138°55.9′W, trapped, 220 m, 2.12.1989 : 1 ♂ 54.0 × 37.3 mm (USNM). Mururoa, Stn 313, 21°52.3′S, 139°02.2′W, trapped, 140 m, 17.10.1990 : 1 ♀ 45.6 × 32.0 mm (USNM). — **Austral Islands** : Maria, Stn 352, 21°47.6′S, 154°42.9′W, trapped, 120 m, 8.12.1990 : 1 ♂ 56.7 × 40.9 mm (QM W8031). Tubuai, Stn 350, 23°20.7′S, 147°32.4′W, trapped, 200 m, 5.12.1990 : 1 ♀ 52.3 × 37.5 mm (MNHN).

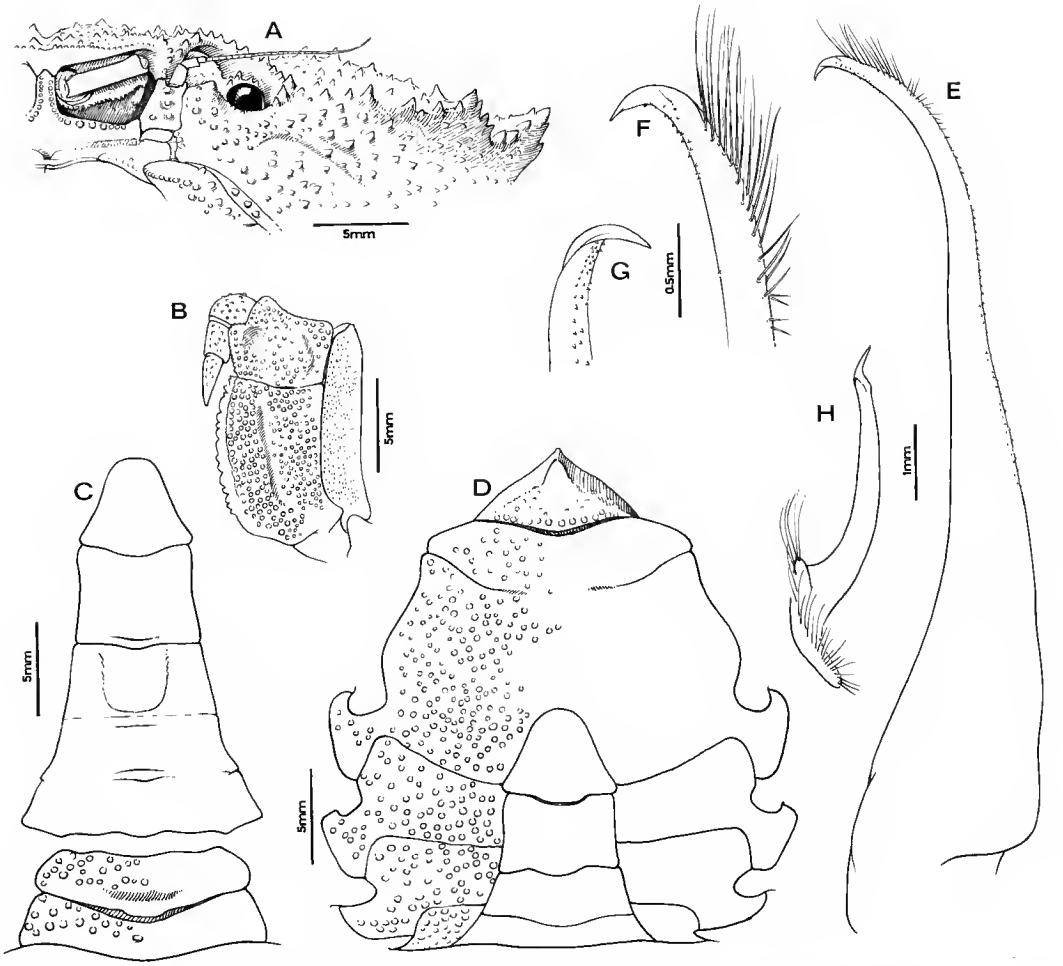

FIG. 2. — *Demania garthi* Guinot and Richer de Forges, 1981. ♂, MNHN-Unreg., Mururoa, Tuamotu Archipelago, 30.11.1989. A, frontal view ; B, third maxilliped ; C, abdomen ; D, sternum and abdomen ; E, F, G, first gonopod ; H, second gonopod.

REMARKS. — This large distinctive species was described from a single female specimen ; therefore an opportunity is taken here to illustrate the male for the first time.

COLOUR. — Predominantly reddish-orange on carapace and pereiopods, with cream to white mainly in the grooves separating the regions, but also lightly speckled elsewhere. Chelae with fingers reddish-orange basally, followed by a broad, brown band, fading to a dirty cream on distal half.

DISTRIBUTION. — Southern Pacific Ocean from New Caledonia (type locality) to French Polynesia. These records mark a considerable easterly range extension. Bathymetric range : 200-245 m.

Demania mortenseni (Odhner, 1925) comb. nov.
(Fig. 3 ; pl. 3)

Actaea mortenseni Odhner, 1925 : 51-52, pl. 5, fig. 9. (?) SAKAI, 1976 : 442-443, pl. 158, fig. 1.
[*Actaea*] *mortenseni* ; GUINOT, 1976 : 204, pl. 19, fig. 4, 4a.

MATERIAL EXAMINED. — **French Polynesia**. SMCB (J. POUPIN) : **Marquises Islands** : Fatu Hiva, Stn 306, 10°31.1'S, 138°39.4'W, trapped, 250 m, 4.09.1990 : 1 ♀ 21.4 × 15.7 mm ; 2 ♂ 20.9 × 15.0, 19.7 × 14.3 mm (MNHN-B22249). — **Society Islands** : Iles Sous le Vent, Mopelia, 16°47.0'S, 153°55.8'W, depth unknown, 9.08.1989 : 1 ♂ 21.5 × 15.0 mm (USNM). — **Tuamotu Archipelago** : Akiaki, 18°32'S, 139°12'W, 250-300 m, in pots, 10.06.1989 : 1 ♂ 19.5 × 14.0 mm (MNHN-B22248) 1 ♂ 18.0 × 12.7 mm (QM W8032). Mururoa, 21°46.8'S, 138°52.1'W, 200 m, caught in pots, 28.11.1989 : 1 ♀ 17.9 x 12.4 mm (MNHN-B22250). Tuamotu Arch., 350 m, caught in pots, 8.07.1985 : 1 ♀ 24.1 × 16.6 mm (USNM).

DESCRIPTION

Carapace transversely ovoid ; *c.* 1.38-1.44 times broader than long. Fronto-orbital width *c.* 0.75-0.8 times carapace length. Carapace convex anteriorly, flat from side to side across postero-branchial regions. Regions well defined, separated by smooth grooves ; 1F and 2F fused ; 1M moderately large, triangular, separated from 2M ; 2M large, broad not subdivided ; 3M entire, medial prolongation narrow, reaching nearly to anterior end of 1M ; 4M distinguishable ; 1L, 2L, and 3L fused into single, broad region ; 4L separated anteriorly from 1L-3L by a shallow groove, fused with 5L laterally ; 6L poorly separated from 5L ; 1P broad, poorly delimited laterally ; 2P also poorly defined, but with ridges slightly raised laterally above posterior margin. Anterolateral margins regularly convex, granular ; with three low teeth behind the exorbital angle ; not strongly projecting ; first tooth about half-way back along anterolateral margin ; in front of first tooth and lateral to orbit, margin rounded, not defined ; second and third teeth evenly spaced, slightly more prominent than first ; greatest carapace width between second pair of teeth ; posterolateral margins convergent, straight. Front *c.* 0.29-0.33 times carapace width ; 0.56-0.6 times fronto-orbital width ; bilobed, margins acutely granular ; lateral angles formed by acute large granules. Posterior margin *c.* 0.35-0.37 times carapace width. Carapace surface covered in rounded granules, except in grooves separating regions ; larger anteriorly, minute posteriorly ; more acute towards margins, especially on smaller specimens ; without setae. Upper orbital border evenly granular ; concave ; orbital fissures obsolete. Lower orbital border irregularly granular. Inner angle of lower orbital border formed by a triangular tooth ; lateral edge of orbit without a notch. Antennal flagellum entering orbit, filamentous, reaching just beyond outer orbital margin. Basal antennal segment just touching front. Basal antennular segment with row of granules along anterior margin and a short row anterolaterally ; palp folds obliquely, first segment moderately long, armed with small sharp granules on outer face ; inter-antennular septum triangular ; superior margins of epistome below antennules with a row of granules, inferior margin projecting.

Third maxilliped : merus of third maxilliped distinctly shorter than ischium. Merus *c.* 0.7

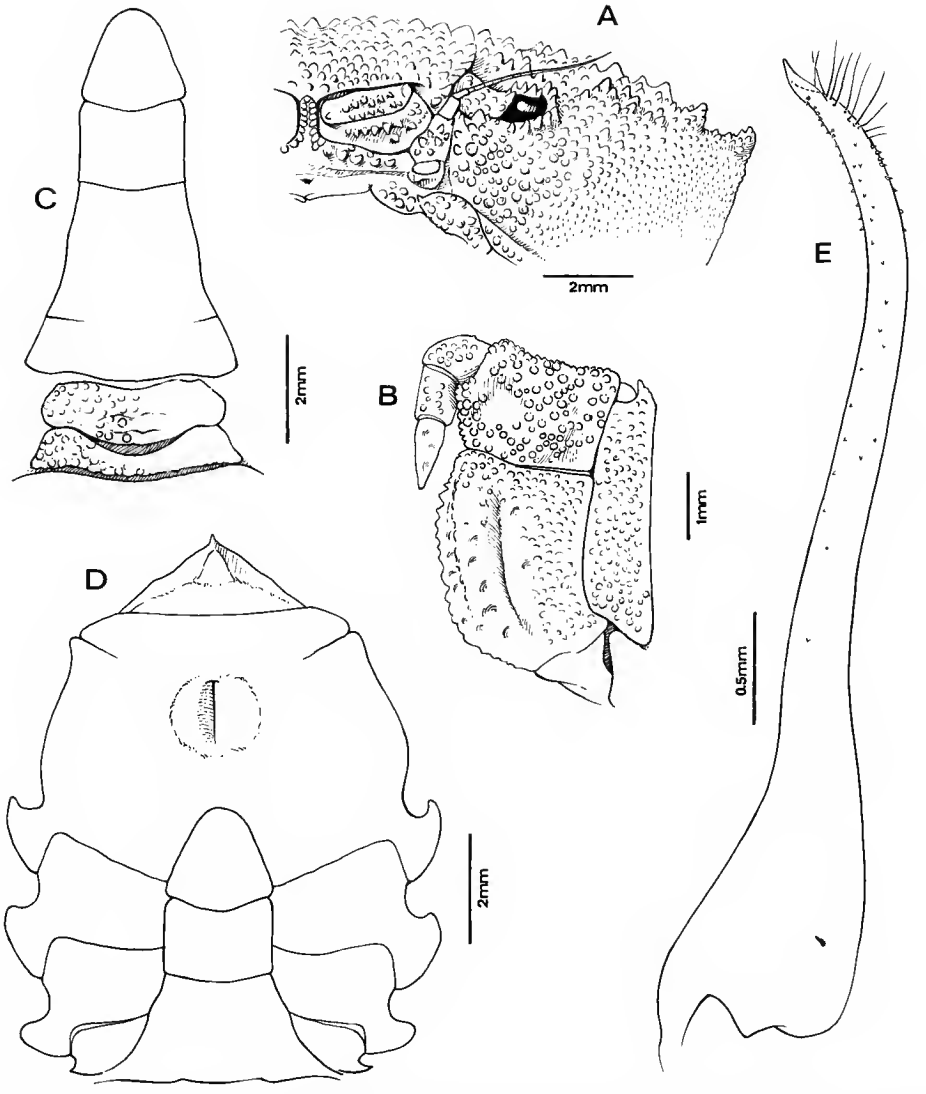

FIG. 3. — *Demania mortenseni* (Odhner, 1925). ♂, MNHN-B22248, Akiaki, Tuamotu Archipelago. A, frontal view ; B, third maxilliped ; C, abdomen ; D, sternum and abdomen ; E, first gonopod.

times wider than long ; antero-external angle produced, strongly angled, rounded ; 0.5-0.6 times length of ischium. Ischium sub-rectangular, length *c.* 1.3-1.5 times width ; inner margin granular.

Chelipeds subequal ; large and robust, height of palm *c.* 0.55 times length including fixed finger ; merus with posterior border granulate, with broad subdistal lobe ; lower border

angle, connected by an oblique crest to a small ventral tubercle ; inner margin granular ; upper and outer surfaces covered with conical granules. Outer surface of palm with coarse conical granules. Outer surface of palm without setae. Inner surface of palm sparsely granular, most granules minute, smooth, small patch of larger granules medially. Immovable finger with ventral granular ridge ; moderately short. Length cutting edge *c.* 0.34 times length propodus. Ventral border of chela more-or-less concave at base of fixed finger. Dorsal surface of dactyl granular. Fingers pointed ; a narrow gape between cutting margins basally.

Walking legs of medium length ; compressed ; slender ; first and second pairs sub-equal and longer than others, very slightly longer than third pair. Longest leg *c.* 1.2 times maximum carapace width. Merus of third leg *c.* 2.9-3.3 times as long as wide. Carpus *c.* 2-2.3 times as long as wide. Propodus *c.* 1.6-1.9 times as long as wide. Dactyli *c.* 1.4-1.5 times length of propodus. Dactyli slender and straight ; terminating in an acute chitinous recurved tip. Merus of anterior margin terminating in a pronounced blunt tooth. Superior margins of meri with row of bluntly acute, distally pointed tubercles, appearing serrated ; inferior margins granular, particularly on anterior legs ; carpi and propodi with enlarged, coarse, bluntly acute tubercles on superior margins, reducing in size across upper face, more-or-less arranged in rows ; bearing scattered setae on margins, and forming a conspicuous row on distal inferior margins of propodi and on upper and lower margins of dactyli.

Male abdomen relatively narrow ; five free segments ; third to fifth fused ; first segment subequal in width to third. First segment narrow. Segments three-five tapering. Segment six *c.* 1.2-1.3 times wider than long. Telson longer than segment 6 ; triangular, rounded apically, about as long as wide at base.

Gonopods : G1 long, reaching well past suture between sternites 4 and 5 ; slender ; curved. Setae present ; row of long setae on dorsal margin near tip ; minute conical setae along dorsal margin over distal half, and on ventral margin near tip ; tip pointed, hollowed, gonopore opening subterminally. G2 short ; evenly curved ; tip short, reflexed, pointed.

Sternum smooth, punctate ; with short, deep cleft medially on sternite 4, just behind line of fusion with sternite 3.

Remarks

The present specimens agree precisely with the published descriptions and figures in Odhner (1925, pl. 5, fig. 9) and the photograph of the holotype in Guinot (1976, pl. 19, fig. 4, 4a). The pattern of dorsal carapace regions, the degree of granulation, the shape of the front, and the length and armature of the legs (as can be seen on Odhner's figure), all leave no doubt that the identification is correct. The record of Sakai (1976) needs to be confirmed — the shape of the anterolateral margins of the specimen he figured is appreciably different from the holotype and from specimens in the present series. The male has not been previously described, helping to explain why its correct generic placement has been problematical. Guinot (1976) removed it both from *Actaea* and the Actaeinae without giving it a new generic position, except to say that it was more nearly related to *Xanthias* and its allies. In this I agree, and further suggest that it should rightfully belong to *Demania* Laurie, 1906. This genus has grown enormously in the last 20 years and now includes about 17 species (see Ng and Yang, 1989, for a key to currently recognised species). The generic definition is, however, rather broad, and

a careful review of the included species may reveal natural groupings within it, and lead to the splitting of the genus. The type of the genus, *Demania splendida* Laurie, 1906, is very distinctive and there seems to be a natural grouping around it of species, all having the superior margins of the meri of the walking legs smoothly crested. The present species although not part of this group, nevertheless has its closest relatives amongst the currently recognised *Demania* species and is therefore included in this genus.

By having serrated dorsal margins of the meri of the walking legs, by the shape of the carapace and the frontal margin, and by having the dorsal surface of the carapace covered with small pointed granules, *Demania mortenseni* most closely resembles *D. crosnieri* Serène, 1984, *D. serenei* Guinot and Richer de Forges, 1981, *D. garthi* Guinot and Richer de Forges, 1981, and *D. alcocki* Deb, 1986. It is separated from the former two by having region 2M entire, and not longitudinally divided. It differs obviously from *D. alcocki* by having spiniform anterolateral teeth and small, sharp granules covering the carapace and legs. It is closest in appearance to *D. garthi* but it can be separated by several characters : the less prominent anterolateral spines ; the deflexed frontal margin with the evenly convex lobes, whereas on *garthi* the frontal margin is more projecting and the lobes more sinuous ; the walking legs, and in particular the meri are relatively shorter ; the fingers of the chelipeds are shorter ; the male first pleopods differ ; and finally, *mortenseni* is a much smaller species. The regional definition is almost identical on both species, and the shapes of the sternums and male abdomens are very similar. *D. mortenseni* resembles members of the Actaeinae in the shape of the deflexed and rounded frontal margin, and in the relatively short fingers of the chelipeds, but these could be considered convergences, as the other similarities to the Xanthinae are so great.

Distribution. — Kei Islands, Micronesia, (5°37'10'S, 132°23'W), type locality, to Tuamotu Archipelago, French Polynesia (21°47'S, 138°52'W). Bathymetric range : 200-350 m.

PARAXANTHODES Guinot, 1968

Paraxanthodes Guinot, 1968*a* : 723-726 ; 1971 : 1069. Sakai, 1976 : 432. Serène, 1984 : 208-209.

Paraxanthodes Guinot, 1968, was established to receive two species : *Micropanope obtusidens* Sakai, 1965 (type species), and *Xanthodes cumatodes* McGilchrist, 1905. The description of *Paraxanthodes polynesiensis* sp. nov. brings the total to three. The new species is quite distinctive, differing markedly from the two already known species, but these differences are mostly superficial and not of generic significance. An updated generic diagnosis is given.

Diagnosis. — Carapace transversely oval or hexagonal, c.1.4-1.5 times wider than long ; regions well defined ; 1M fused to inner branch of 2M ; 2M partially divided into three parts by longitudinal grooves, outer groove more-or-less obvious ; 4M more-or-less distinct ; surface may be coarsely granular and roughened, or minutely granular ; front slightly to moderately projecting, bilobed, lobes well separated or abutting for most of length, lateral angles of front projecting ; anterolateral margins with 4 teeth behind exorbital angle, surface adjacent to orbit rugose and granular, first tooth may be connected by granular ridge with orbit (*polynesiensis*) otherwise margin poorly defined and continuing onto sub-hepatic region sometimes with 1-2 larger granular tubercles, posterolateral borders strongly convergent. Merus of third maxilliped with antero-external angle produced. Efferent branchial ridges extending anteriorly to meet

epistome ; lacinie of maxilliped 1 with inner expansion relatively short and truncated. Chelipeds moderately unequal, similar in form but smaller cheliped more slender and with fingers longer ; fingers pointed. Walking legs moderately long, compressed, with superior margins varying from minutely granular to serrated, and sometimes slightly cristate. Male abdomen relatively narrow, third to fifth segments fused. Telson rounded. Male gonopod 1, long, slender, curved, tip reflexed and more-or-less elongated.

Paraxanthodes polynesiensis sp. nov.
(Fig. 4 ; pl. 4)

ETYMOLOGY. — Named in reference to Polynesia, from where the only specimens are so far known.

TYPE MATERIAL. — The male, 20.8 × 15.1 mm, from Tuamotu Archipelago, is designated the holotype. All other specimens are paratypic.

MATERIAL EXAMINED. — **French Polynesia**. SMCB (J. POUPIN) : **Marquises Islands** : Tahuata, Stn 300, 9°54.5'S, 139°07.9'W, trapped, 190 m, 1.09.1990 : 2 ♀ 24.4 × 17.5, 22.6 × 16.7 ; 1 ♂ 32.5 × 23.6 mm (MNHN-B22227). Fatu Hiva, Stn 306, 10°31.1'S, 138°39.4'W, trapped, 250 m, 4.09.1990 : 1 ♀ 19.3 × 14.2 mm (MNHN-B22226). — **Tuamotu Archipelago** : Mururoa, 21°46.8'S, 138°52.1'W, trapped, 200 m, 28.11.1989 : 1 ♂ 20.8 × 15.1 mm (MNHN-B22225)

DESCRIPTION

Carapace transversely ovoid, *c.* 1.38-1.39 times broader than long. Fronto-orbital width *c.* 0.67-0.75 times carapace length. Carapace convex anteriorly, flat from side to side across posterobranchial regions but depressed laterally. Regions well defined : 1F and 2F not demarcated ; 1M fused with inner branch of 2M posteriorly, anterior margin prominent, straight, slightly oblique ; 2M partially divided by a broad longitudinal groove, outer branch about twice width of inner branch, outer branch itself partly sub-divided by a shallower short, narrow groove with outer part narrower than inner part ; 3M entire, reaching to about middle of 1M ; 4M not strongly separated ; 2L, 4L, and 5L all clearly separated, 4L confluent laterally with third anterolateral tooth ; 6L poorly and incompletely separated from 5L by shallow grooves ; cardiac region (1P) relatively broad, oval, moderately well defined by shallow grooves ; intestinal region narrow. Anterolateral margins regularly convex ; cristate ; with four teeth behind the exorbital angle ; teeth evenly spaced, all of similar size and broadly triangular, third tooth slightly the largest ; first tooth well separated from, and slightly behind, orbit, connected to exorbital angle by a bluntly rounded crest ; below this crest, lateral to orbit, surface uneven with raised clumps of granules ; posterolateral margins oblique, straight, about same length as anterolateral margins. Front *c.* 0.28-0.31 times carapace width ; *c.* 0.56-0.57 times fronto-orbital width ; not deflexed, strongly projecting ; bilobed, lobes straight and oblique laterally, or moderately convex ; lobes abutting and fused over most of length but with obvious median incision ; lateral angles rounded, narrow, noticeably produced. Posterior margin *c.* 0.4-0.5 times carapace width, relatively wider in females. Carapace surface entirely covered with minute rounded granules except for central part of grooves ; without setae. Upper orbital border minutely granular ; concave ; lateral truncate tooth formed by fused lateral fissures. Lower orbital border of inner angle formed by a triangular tooth ; a second, similar-sized tooth laterally ; with V-shaped notch at outer edge. Antennal flagellum small and entering orbit, fine, reaching a little beyond outer orbital edge. Basal antennal segment just

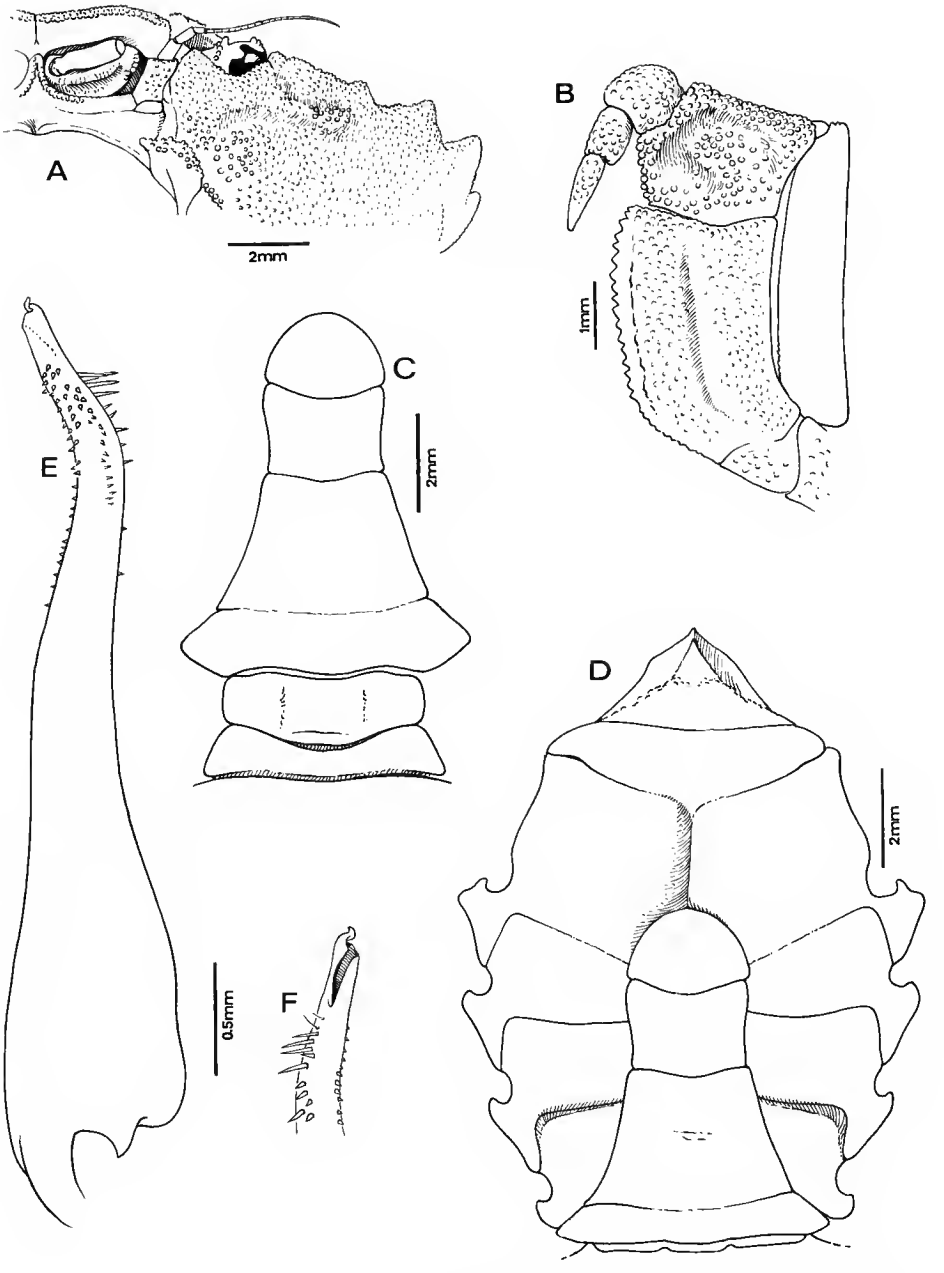

FIG. 4. — *Paraxanthodes polynesiensis* sp. nov. Holotype ♂, MNHN-B22225, Mururoa, Tuamotu Archipelago. A, frontal view ; B, third maxilliped ; C, abdomen ; D, sternum and abdomen ; E, F, first gonopod.

touching front. Basal antennular segment relatively broad, with raised minutely granulate rim on superior and lateral margins ; first segment of palp moderately long, granulate on outer surface, palp folding obliquely ; epistome relatively flat, lower margin not strongly produced ; inter-antennular septum triangular, with margins raised and minutely granular.

Third maxilliped : merus distinctly shorter than ischium, wider than long, length *c.* 0.75 times width ; outer surface granulate ; antero-external angle produced, rounded ; 0.5 times length of ischium. Ischium sub-rectangular, length *c.* 1.7 times breadth.

Chelipeds noticeably unequal, either may be larger ; large and robust ; palm height *c.* 0.5 times length including fixed finger. Merus with posterior border convex, coarsely granulate ; lower border microscopically granulate, rounded ; anterior border minutely granulate, rounded ; carpus with a broad tooth at inner angle ; a second, smaller granular tooth, ventro-proximally ; inner margin minutely granular ; upper and outer surface rugose, minutely granular. Outer surface of palm smooth and punctate ventrally, becoming minutely granular and slightly vertically striated dorsally ; a strong, broad, longitudinal, sub-dorsal groove ; and a narrow longitudinal groove along superior margin visible from above. Outer surface of palm without setae. Inner surface of palm smooth. Immovable finger long (smaller chela with fingers longer than major chela) ; with ventral ridge. Length of cutting edge *c.* 0.4 times length of propodus. Ventral border of chela concave at base of fixed finger. Dorsal surface of dactyl smooth, rounded, punctate. Fingers pointed, tips curved ; a narrow gape between cutting margins.

Walking legs of medium length ; compressed ; first three pairs all of similar length, *c.* 1.1-1.2 times maximum carapace width. Merus of third leg *c.* 2.8-3.4 times as long as wide. Carpus *c.* 2.2-2.4 times as long as wide. Propodus *c.* 1.4-1.9 times as long as wide. Dactyli *c.* 1.5-1.9 times length of propodus. Dactyli slender, straight, with a strong, longitudinal, lateral furrow ; terminating in an acute chitinous recurved tip. Merus anterior margin terminating in a blunt tooth. Carpus with accessory carinae on upper surface, superior margin of carpus moderately carinate on last leg, but less so on anterior legs. Meri with coarse granules along superior margin, with band of smaller granules on inferior surface ; other segments covered in minute granules. Setae mostly sparse and on margins ; but forming a thick, short tomentum proximally, and on inferior margin of propodi ; and on dactyli except for lateral grooves.

Male abdomen relatively narrow ; five free segments ; third to fifth fused ; third segment the widest. First segment 0.85 times width of third segment. Segments three-five tapering. Segment six *c.* 1.4-1.6 times wider than long. Telson *c.* 0.75 times longer than wide ; evenly rounded.

Gonopods : G1 medium length, not quite reaching suture between sternites 4 and 5 ; moderately stout, moderately compressed, ventro-medially slightly lamelliform ; curved ; tip slightly recurved, tapering to very fine point ; row of stout setae present on dorsal margin behind tip ; minute conical setae on distal half of dorsal margin, and ventrally near tip. G2 short ; evenly curved ; tip short, reflexed, pointed.

Sternum evenly covered in minute granules, male sternum with short medial longitudinal incision on segment four.

Colouration. — On preserved material, colour predominantly orange-brown ; a broad band of reddish pink on pterygostome above base of chelipeds ; fingers blackened, dark colour not extending onto palm.

REMARKS. — *Paraxanthodes polynesiensis* sp. nov. is easily separated from the other two species, *P. obtusidens* (Sakai) and *P. cumatodes* (McGilchrist) by having : the dorsal surface of carapace very finely granular, rather than coarsely granular ; the regions lower and less strongly swollen ; the front less deflexed, more projecting and lamelliform, with the median incision less obvious ; and the unarmed walking legs.

DISTRIBUTION. — Known only from French Polynesia, between the Marquises Islands in the north and the Tuamotu Archipelago in the south. Bathymetric range : 190-250 m.

EUXANTHINAE Alcock, 1898

ALAINODAEUS gen. nov.

ETYMOLOGY. — Named in honour of Alain CROSNIER, using his first name in combination with " daeus " from *Medaeus*.

TYPE SPECIES. — *Alainodaeus akiaki*, by original designation. Gender is masculine.

DIAGNOSIS. — Carapace transversely ovoid, *c.* 1.4-1.6 times broader than long. Regions moderately defined ; 2M at least partially divided longitudinally, outer branch very broad and rounded. Anterolateral margins with four teeth behind exorbital angle ; margin anterior to first tooth poorly defined. Front *c.* 0.25-0.35 times carapace width ; moderately deflexed, not projecting ; bilobed, with small but obvious, blunt, medial and lateral teeth. Posterior margin *c.* 0.35-0.45 times carapace width. Upper orbital border concave, lateral fissures obvious or only slightly indicated. Lower orbital border with an inner and outer triangular tooth ; with V-shaped notch at outer edge. Antennal flagellum relatively small and entering orbit. Basal antennal segment just touching front. Basal antennular segment relatively broad, with raised granular rim across upper and lateral margins ; second segment relatively long ; palp folding horizontally. Interantennular septum relatively broadly triangular, with lateral margins only slightly concave. Third maxilliped with merus *c.* 0.5 times length of ischium ; wider than long, antero-external angle slightly produced. Palp articulating at inner distal margin of merus. Chelipeds large and robust ; markedly unequal, carpus with a broad spine at inner angle ; 1-3 smaller spines ventro-proximal to major spine. Ventral border of chela concave at base of fixed finger. Fingers pointed, tips recurved ; without a noticeable gape between cutting margins. Walking legs relatively long ; slightly flattened ; slender. Merus of anterior margin terminating in a blunt tooth ; dactyli slender, straight, and flattened, with an acute, chitinous tip. Male abdomen relatively narrow ; five free segments ; third to fifth fused. Male first gonopod of medium length ; stout ; broadly flanged over proximal two-thirds, quickly tapering distally ; without long setae. Sternum relatively broad ; fused sternites 3-4 with deep, median, longitudinal cleft.

REMARKS

The two species included in this new genus are *Alainodaeus akiaki* sp. nov. and *A. rimatara* sp. nov. *Alainodaeus* species are most closely allied to those of *Monodaeus* and *Medaeops*, both in the general form of the carapace and more specifically by the shape of the male first pleopod which has a lateral flange over its proximal two-thirds and then narrows abruptly [see GUINOT, 1967, figs 37 and 40, for *Monodaeus tuberculidens* (Rathbun) and *Medaeops granulosus* (Haswell) respectively].

Alainodaeus differs from both those genera by the following characters : 1, the regions of the carapace are less well defined, and differ in shape — in particular, 2M is much larger and broader, less obviously longitudinally divided, and the outer half is much wider than the inner half ; 2, the frontal margin is not straight but consists of a pair of small median prominences and a pair of broad, moderately convex lateral lobes ; 3, the epistome is different in shape, with the upper margins below the antennules being less concave, so that the inter-antennular septum is more broadly triangular ; 4, the sixth segment of the male abdomen is much broader in comparison to its length (almost 2 times) and the margins are subparallel, whereas in the other two genera it is relatively longer *c.* 1.4-1.6 times, and tends to be noticeably wider distally ; 5, the walking legs are relatively much longer and very slender, a condition approached only by *Monodaeus rouxi* (Capart) ; 6, the fingers of the minor cheliped are very long, noticeably longer than in the related genera ; 7, the male first pleopod lacks long setae terminally.

Besides the above unique characters shared by the two new species, *Alainodaeus* further differs from *Monodaeus* by the shape and size of the lacinia of the endopodite of maxilliped 1. In *Monodaeus* it is large and expanded towards the medial line of the roof of the buccal cavity ; but in *Alainodaeus* (like in *Medaeops*) it is much smaller and confined to the lateral part of the buccal cavity, where it lies against the strongly defined ridge of the efferent branchial channel. This ridge is poorly indicated in *Monodaeus* and also closer to the medial line.

Alainodaeus further differs from *Medaeops* by having the front not or only slightly projecting, and having the second segment of the antennules much longer and folding almost horizontally. *Medaeops* typically has a noticeably projecting frontal margin and the antennules are rather short and fold more obliquely (see for comparison GUINOT, 1967, fig. 21).

Alainodaeus differs from *Paramedaeus* in many characters. In particular, *Paramedaeus* has subequal chelae ; a different type of male first pleopod with the tip bearing long setae (see SERÈNE, 1984, figs 50, 51) ; and much more projecting carapace regions.

Alainodaeus akiaki sp. nov.

(Fig. 5 ; pl. 5)

ETYMOLOGY. — Named after Akiaki Island, part of the Tuamotu Archipelago, in French Polynesia. It is treated here as a noun in apposition.

TYPE MATERIAL. — The male (MNHN-B22243) from Rurutu Island, Austral Islands, is designated holotype. All other specimens examined are paratypic.

MATERIAL EXAMINED. — **French Polynesia**. SMCB (J. POUPIN) : **Tuamotu Archipelago** : Akiaki, 18°32′S, 139°12′W, 250-300 m, in pots, 10.06.1989 : 2 ♂ 33.8 × 22.6 mm, 36.7 × 23.6 mm (MNHN-B22241). — **Austral Islands** : Maria, Stn 352, 21°47.6′S, 154°42.9′W, trapped, 120 m, 8.12.1990 : 1 ♂ 32.5 × 20.9 mm (QM W8035). Rurutu, 22°27.8′S, 151°22.9′W, 230-240 m, caught in pots, 10.03.1989 : 1 ♂ 29.2 × 19.4 mm (MNHN-B22243). *Ibid.* 1 ♂ 27.9 × 18.2 mm (MNHN-B22242). Rimatara, 22°38.2′S, 152°49.7′W, 300 m, caught in pots, 11.03.1989 : 1 ♂ 29.2 × 19.4 mm (MNHN-B22240). Raivavae, 23°51.4′S, 147°44.5′W, 350 m, caught in pots, 1.03. 1989 : 1 ♂ 34.4 x 22.2 mm (USNM).

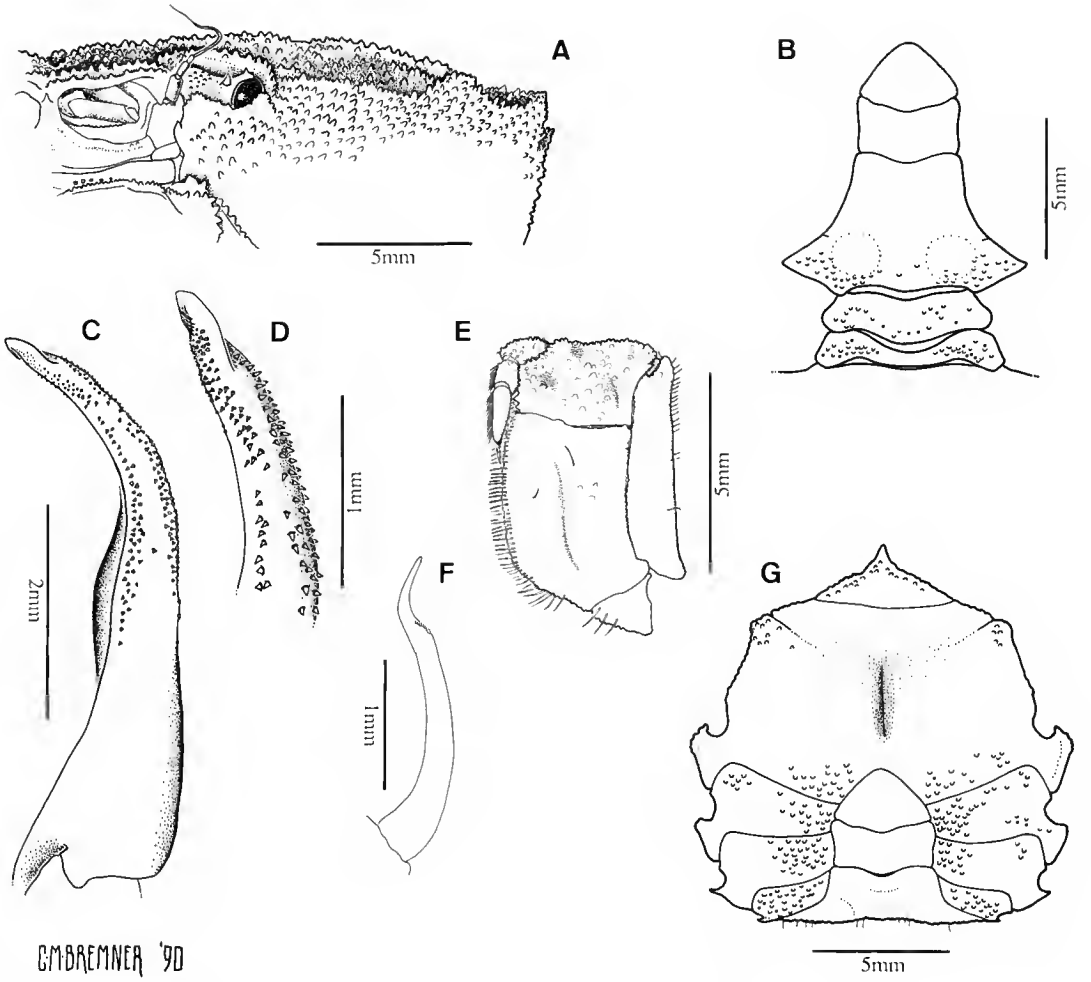

FIG. 5. — *Alainodaeus akiaki* gen. nov., sp. nov. Holotype ♂, MNHN-B22243, Rurutu, Austral Islands. A, frontal view ; B, abdomen ; C, D, first gonopod ; E, third maxilliped ; F, second gonopod ; G, sternum and abdomen.

DESCRIPTION

Carapace transversely ovoid, *c.* 1.5-1.6 times broader than long. Fronto-orbital width *c.* 0.7 times carapace length. Carapace moderately vaulted ; strongly convex longitudinally over anterior third, only slightly from side to side. Regions moderately defined ; 2M separated from 3M and 2M partially divided longitudinally by a short, shallow, ill-defined groove, outer branch of 2M very broad and rounded, *c.* twice width of internal branch ; 1F and 2F not differentiated ; 1M fused to internal branch of 2M ; 4M not clearly distinguishable ; 1L and 3L

not differentiated ; 2L and 4L distinct ; 5L and 6L also distinct, partially fused ; 1P and 2P more-or-less obvious ; 1R, 2R, 3R not distinguishable. Anterolateral margins regularly convex ; with four teeth behind the exorbital angle ; margins granular, first tooth not prominent, situated a little behind and well separated from orbit ; anterior to first tooth clear marginal definition lost, a slight indication of a granular row connecting with orbit and a second continuing obliquely below orbit ; second tooth broadly triangular, third tooth most prominent and sharply pointed, fourth tooth similar to third, but smaller ; greatest carapace width between third anterolateral teeth, but distance between fourth teeth only slightly less. Front *c.* 0.25 times carapace width ; *c.* 0.55 times fronto-orbital width ; moderately deflexed, not projecting ; bilobed, with small, but obvious, blunt, medial and lateral teeth, convex between ; pre-orbital teeth present, bluntly granular. Posterior margin *c.* 0.35-0.4 times carapace width. Surface of carapace granulate except in furrows separating regions ; granules slightly larger and more widely spaced anteriorly ; without setae. Upper orbital border concave, evenly granular, lateral fissure obsolete, slightly indicated. Lower orbital border evenly granular ; inner angle formed by a triangular tooth ; a second, bluntly granular tooth laterally ; with V-shaped notch at outer edge. Antennal flagellum small and entering orbit, reaching slightly farther than lateral edge of orbit. Basal antennal segment just touching front. Basal antennular segment relatively broad, with raised granular rim across upper and lateral margins ; second segment relatively long ; palp folding horizontally. Inter-antennular septum moderately wide basally ; inner margins of antennular fossae oblique and only moderately concave ; interantennular septum relatively broadly triangular ; lower margin of epistome slightly projecting as thin rim.

Third maxilliped : merus *c.* 0.5 times length of ischium ; wider than long, length *c.* 0.7 times width ; antero-external angle slightly produced, rounded. Ischium rectangular ; inner margin granular. Palp articulating at inner distal margin of merus.

Chelipeds large and robust ; markedly unequal, right cheliped the larger on all present specimens ; minor cheliped of similar form but more slender and with longer fingers ; merus with posterior border sharply granulate ; without distinct subdistal spine ; lower border armed with spinules ; frontal face of merus armed with sharp granules ; small spines especially near upper and lower margins ; carpus with a broad spine at inner angle ; inner margin armed with small spines, at least 1 and sometimes 2-3 smaller prominent spines ventro-proximal to major spine ; outer margin and upper surface granular. Outer surface of palm coarsely granular ; without setae. Inner surface of palm granular, granules finer than on outer surface ; also with a row of 4-6 inwardly directed spines on inner edge of superior margin ; and an uneven row of more numerous spines on ventral margin continuing along bottom edge of fixed finger nearly to beginning of darker colouring ; a third longitudinal row of more prominent sharp granules below middle of inner surface. Immovable finger long, rounded on outer surface ; with ventral ridge extending from base to tip ; length of cutting edge *c.* 0.4 times length of propodus on major chela, *c.* 0.5 on minor chela. Ventral border of chela concave at base of fixed finger. Dorsal surface of dactyl finely granular. Fingers pointed, tips fine and markedly recurved ; cutting margin of immoveable finger with 4 prominent triangular teeth, evenly spaced, sharply pointed on minor chela, blunt on major chela ; cutting margin of dactyl with 3 prominent triangular teeth in the proximal half and a fourth less clearly differentiated tooth in distal half, teeth better developed on major chela ; without a noticeable gape between the cutting margins.

Walking legs relatively long ; slightly flattened ; slender ; second and third pairs sub-equal, longer than others, *c.* 1.3 times maximum carapace width. Merus of third leg *c.* 4-4.6 times as

long as wide. Carpus *c.* 2.5-3 times as long as wide. Propodus *c.* 2.3-2.7 times as long as wide. Dactyli *c.* 1.2 times length of propodus. Dactyli slender, straight, and flattened ; terminating in an acute chitinous tip. Merus anterior margin terminating in a blunt tooth. Carpus with accessory carinae on upper surface. All segments granular, with slightly more prominent row of spinules along upper margins of meri, and on antero-ventral borders, particularly of first two pairs ; granules generally sharper on carpi and propodi ; setae generally lacking, but very short, sparse setae between granules on carpi and propodi, which become slightly longer and thicker and completely cover dactyli.

Male abdomen relatively narrow ; five free segments ; third to fifth fused ; third segment widest. First segment *c.* 0.8 times width third segment. Segments three-five tapering. Segment six *c.* 1.8-1.9 times wider than long. Telson *c.* 0.65-0.7 times longer than wide ; slightly longer than sixth segment ; bluntly pointed and triangular.

Gonopods : G1 medium length ; stout ; broadly flanged over proximal two-thirds, quickly tapering distally to a bluntly acute, slightly twisted tip ; without long setae, bearing only minute bristles on distal half. G2 moderately long ; evenly curved ; tip short, recurved.

Sternum relatively broad ; fused sternites 3/4 with deep median, longitudinal cleft.

Distribution. — Known only from French Polynesia, from Tuamotu Archipelago, 18°32′S, 139°12′W, to the Austral Islands, 23°51.4′S, 147°44.5′W. Bathymetric range : 230-350 m.

Alainodaeus rimatara sp. nov.

(Fig. 6 ; pl. 6)

Etymology. — Named after Rimatara, part of the Austral Islands Group, in French Polynesia. It is treated here as a noun in apposition.

Type material. — The male 22.4 × 15.3 mm (MNHN-B22244) is the holotype. All other specimens listed are paratypes.

Material examined. — **French Polynesia**. SMCB (J. Poupin) : **Tuamotu Archipelago** : Takapoto, 14°40.0′S, 145°15.2′W, trapped, 250 m, 7.06.1989 : 1 ♂ 15.9 × 12.0 mm, 1 ♀ 17.4 × 12.1 mm (USNM). Hao, Stn 246, 18°04.5′S, 141°01.6′W, trapped, 90 m, 2.06.1990 : 1 ♂ 14.6 × 10.0 mm (QM). Akiaki, 18°32′S, 139°12′W, trapped, 250-300 m, 10.06.1989 : 1 ♂ 22.4 × 15.3 mm (MNHN-B22244). Fangataufa, Stn 231, 22°12.0′S, 138°45.9′W, trapped, 270 m, 21.05.1990 : 1 ♀ 16.2 × 11.4 mm (MNHN-B22245). — **Austral Islands** : Rimatara, 22°38.2′S, 152°49.7′W, trapped, 300 m, 11.03.1989 : 1 ♂ 21.8 × 14.6 mm (MNHN-B22247). Raivavae, 23°51.4′S, 147°44.5′W, trapped, 350 m, 1.03.1989 : 1 ♀ 18.0 × 13.2 mm (MNHN-B22246)

Description

Carapace transversely ovoid ; *c.* 1.44-1.5 times broader than long. Fronto-orbital width *c.* 0.89-0.93 times carapace length. Carapace moderately vaulted ; convex longitudinally especially over anterior third, only slightly from side to side. Regions moderately defined ; slightly raised transverse granular rim behind frontal margin, otherwise 1F and 2F not differentiated ; 1M

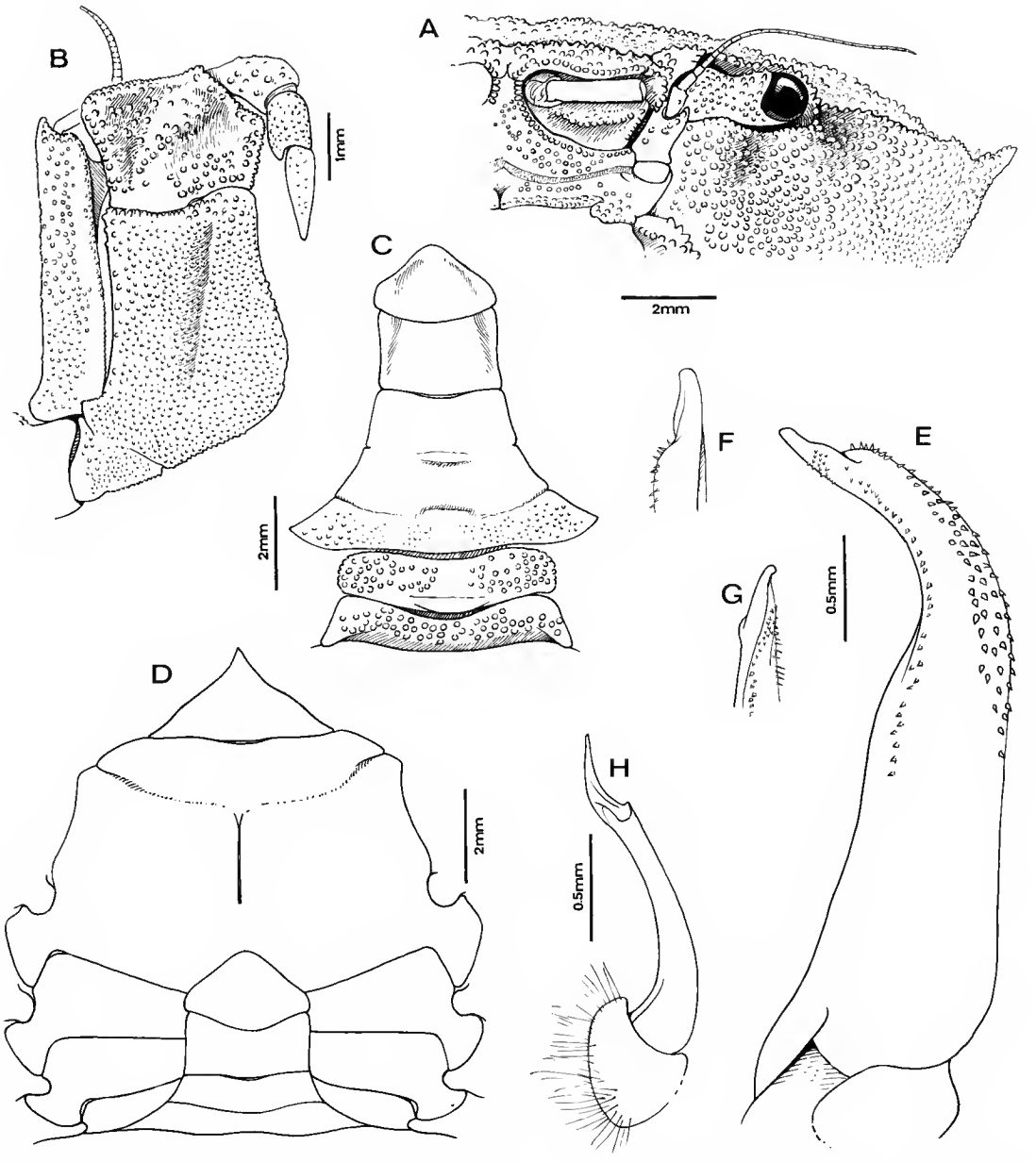

FIG. 6. — *Alainodaeus rimatara* gen. nov., sp. nov. Holotype ♂, MNHN-B22244, Akiaki, Tuamotu Archipelago. A, frontal view ; B, third maxilliped ; C, abdomen ; D, sternum and abdomen ; E, F, G, first gonopod (F, abdominal view of tip ; G, sternal view of tip) ; H, second gonopod.

fused to internal branch of 2M ; 2M separated from 3M ; 2M partially longitudinally divided by a short, shallow ill-defined groove, scarcely apparent on some specimens, outer branch very broad and rounded, *c.* twice width of internal branch ; 4M not clearly distinguishable on most specimens, sometimes present as slightly raised narrow transverse strip on posterior of 3M ; 1L and 3L not differentiated ; 2L and 4L distinct ; 5L and 6L also distinct, partially fused ; 1P and 2P more-or-less obvious ; 1R and 2R not clearly distinct, separated from 3R by shallow groove. Anterolateral margins regularly convex ; with four teeth behind the exorbital angle ; margins granular ; first tooth barely distinct, marked only by slightly raised granules medially on broad convexity lateral to orbit ; margin anterior to first tooth poorly defined, but continuing towards outer edge of orbit ; an area of slightly larger sharper granules continuing obliquely below orbit towards mouth frame ; second anterolateral tooth sharply pointed, forwardly directed ; third tooth more evenly triangular, pointed laterally ; greatest carapace distance between third teeth ; fourth tooth smaller, narrower, set relatively close behind third tooth. Front *c.* 0.33-0.36 times carapace width ; *c.* 0.55 times fronto-orbital width ; moderately deflexed, not projecting ; bilobed, with small but obvious, blunt, medial and lateral teeth ; pointed, granular, pre-orbital teeth present. Posterior margin *c.* 0.37-0.44 times carapace width. Carapace surface granulate except in smooth furrows separating regions ; without setae. Upper orbital border evenly granular, concave, median and lateral fissures obviously indicated. Lower orbital border evenly granular ; inner angle formed by a bluntly pointed, granular lobe ; with second, lower, broader lobe laterally ; with V-shaped notch at outer edge. Antennal flagellum entering orbit, fine, reaching laterally almost to level of second anterolateral tooth. Basal antennal segment just touching front. Basal antennular segment relatively broad, with raised granular rim across upper and lateral margins, upper margin concave, leaving gap when palp folded ; second segment relatively long, palp folding horizontally. Inter-antennular septum moderately wide basally ; inner margins of antennular fossae oblique and only moderately concave ; interantennular septum relatively broadly triangular ; lower margin of epistome slightly projecting as thin rim.

Third maxilliped : merus distinctly shorter than ischium ; wider than long, length *c.* 0.75 times width ; antero-external angle slightly produced, rounded ; *c.* 0.5 times length of ischium. Ischium rectangular ; inner margin minutely granular. Palp articulating at inner distal margin of merus.

Chelipeds large and robust ; markedly unequal, right cheliped normally the larger but on holotype, the left ; minor cheliped of similar form but more slender and with longer fingers. Merus with posterior border tuberculate ; without distinct subdistal spine ; lower border granulate distally ; anterior border coarsely granulate. Carpus with a broad spine at inner angle, armed with accessory spinules ; a second similar but slightly smaller spine ventroproximal to major spine, finer and more acute, also armed with accessory spinules ; outer margin and upper surface granular. Outer surface of palm appearing smooth but microscopically granular ventrally and medially, granules becoming more coarse dorsally and proximally. Outer surface of palm naked. Inner surface of palm appearing smooth, but microscopically granular ; with row of 3-5 inwardly directed small spines on inner edge of superior margin, very obvious in dorsal view. Immovable finger long, rounded on outer surface ; with ventral ridge extending from base to tip ; length cutting edge *c.* 0.4 times length propodus on major chela, *c.* 0.5 on minor chela. Ventral border of chela concave at base of fixed finger. Dorsal surface of dactyl very finely granular, coarser near base. Fingers pointed,

recurved ; minor chela with cutting margins cristate, fixed finger with 3-4 prominent triangular teeth, dactyl with teeth poorly differentiated ; major chela similarly armed but teeth becoming molariform proximally, dactylar teeth well defined, with large, rounded, backwardly directed, peg-like tooth at base ; without a noticeable gape between the cutting margins.

Walking legs relatively long ; compressed ; slender ; third pair the longest, slightly longer than second, *c.* 1.3-1.4 times maximum carapace width. Merus of third leg *c.* 4-4.5 times as long as wide. Carpus *c.* 2.8 times as long as wide. Propodus *c.* 2.7-2.9 times as long as wide. Dactyli *c.* 1.3 times length of propodus. Dactyli slender, straight, flattened ; terminating in an acute chitinous tip. Anterior margin of merus terminating in a blunt tooth. Carpus with accessory carinae on upper surface. All segments granular, with 2 rows of spinules, or sharp granules, along upper borders of meri, anterior row more prominent ; a similar row along anteroventral borders of meri, most obviously on first two pairs ; granules generally sharper on carpi and propodi ; occasional fine setae on borders of segments, more common distally ; short setae on upper and lower borders of propodi and dactyli.

Male abdomen relatively narrow ; five free segments ; third to fifth fused ; third segment the widest. First segment *c.* 0.85 times width third segment. Segments three-five tapering. Segment six *c.* 1.75-1.85 times wider than long. Telson *c.* 0.65 times longer than wide, very slightly longer than sixth segment ; bluntly pointed, rounded.

Gonopods : G1 medium length ; stout, broadly flanged over proximal two-thirds, quickly tapering distally to a bluntly acute, slightly twisted tip ; without long setae, bearing only minute bristles on distal half. G2 moderately long ; evenly curved ; tip short, recurved.

Sternum relatively broad ; fused sternites 3/4 with deep median longitudinal cleft ; surface finely granular.

Remarks. — *Alainodaeus rimatara* sp. nov. differs from *A. akiaki* sp. nov. in several obvious characters. The frontal margin is slightly more prominent and the frontal region less convex ; the first anterolateral tooth is almost obsolete ; the outer face of palm of cheliped bearing only dorsal granulation but otherwise smooth, whereas in *A. akiaki* the outer face is completely covered with granules ; and, similarly, the inner face of the cheliped palm is smooth below the inner dorsal row of spines, and lacks both the median and ventral rows of spinules characteristic of *A. akiaki.*

Distribution. — Known only from French Polynesia, from Tuamotu Archipelago, 14°40.0′S, 145°15.2′W, to the Austral Islands, 23°51.4′S, 147°44.5′W. Bathymetric range : 90-350 m.

EPISTOCAVEA gen. nov.

Etymology. — From ‘epistome’ and the latin *cavea* meaning an excavated hollow place. Gender is feminine.

Type species. — *Epistocavea mururoa* sp. nov., here designated.

Diagnosis. — Carapace transversely ovoid, *c.* 1.4-1.5 times broader than long. Regions moderately defined. Anterolateral margins regularly convex ; more-or-less carinate ; divided into 4 teeth ; continue in

an arc below orbit to meet anterolateral corner of buccal frame ; meri of third maxillipeds sharply angled backwards over distal third, forming a concave shelf, and fitting against epistome, completely sealing buccal cavity ; with maxillipeds in place a continuous convex arc formed with anterolateral margins ; whole region across front from below orbits deeply excavated. Front moderately projecting, with medial notch. Posterior margin *c.* 0.4 times carapace width. Upper orbital border concave ; orbital fissures obsolete. Inner angle of lower orbital border formed by a triangular tooth. Basal segment of antenna broadly in contact with front ; antennal flagellum entering orbit. Basal antennular segment triangular, flagellum folding obliquely. Inter-antennular septum narrow. Chelipeds markedly unequal, large and robust ; carpus with a broad tooth at inner angle and on inner face below inner angle ; ventral border of chela concave at base of fixed finger ; fingers pointed ; a narrow gape between cutting margins. Walking legs of medium length ; flattened ; moderately slender ; second pair the longest ; dactyli stout, straight, and flattened, terminating in an acute, chitinous tip ; anterior margin of merus unarmed terminally. Male abdomen relatively narrow ; five free segments ; third to fifth fused. Male first gonopod of medium length, slender, curved. Sternum relatively broad.

Remarks

Epistocavea clearly belongs to the Euxanthinae because the anterolateral margins do not meet the exorbital angle but continue below the orbit across the sub-hepatic region to meet the buccal frame. It must be placed closest to those genera that have the posterolateral borders relatively longer, less strongly convergent and not strongly hollowed out to receive the walking legs i.e. *Medaeops*, *Medaeus*, *Monodaeus*, *Paramedaeus*. It lacks the strongly defined 4M of *Medaeus*, the relatively slender legs of *Monodaeus*, and has shorter anterolateral margins than *Paramedaeus*.

In overall conformation of the carapace and chelipeds *Epistocavea* most closely resembles species of *Medaeops*. It is easily separated from all related genera by the broad, deeply concave epistome and sub-hepatic regions, and the peculiar shape of the meri of the third maxillipeds.

Epistocavea mururoa sp. nov.

(Fig. 7 ; pl. 7)

Etymology. — Named in reference to the Polynesian name of the type locality. It is treated here as a noun in apposition.

Type material. — The male 29.8 × 20.7 mm from Mururoa Island (MNHN-B22235) is designated the holotype ; all other specimens are paratypes.

Material examined. — **French Polynesia**. SMCB (J. Poupin) : **Society Islands** : Bora Bora, Stn 275, 16°26.5′S, 151°46.2′W, trapped, 190 m, 25.06.1990 : 2 ♂ 28.9 × 20.7, 32.9 × 23.3 mm (MNHN-B22237). — **Tuamotu Archipelago** : Vanavana, Stn 331, 20°45.7′S, 139°10.1′W, trapped, 240 m, 28.10.1990 : 2 ♀ 32.1 × 22.3, 30.0 × 19.7 mm (MNHN-B22236). Mururoa, 21°46.9′S, 138°55.4′W, trapped, 210 m, 30.11.1989 : 1 ♀ 32.0 × 22.8 mm (MNHN-B22234). Mururoa, Stn 222, 21°51.1′S, 138°58.7′W, trapped, 100 m, 15.05.1990 : 1 ♂ 29.8 × 20.7 mm (MNHN-B22235). — **Austral Islands** : Rurutu, Stn 337, 22°28.6′S, 151°21.8′W, trapped, 125 m, 27.11.1990 : 1 ♀ 33.8 × 23.4 ; 4 ♂ 35.6 × 25.3, 38.0 × 27.1, 37.5 × 26.0, 38.3 x 26.6 mm (MNHN-B22239). *Ibid.* 1 ♀ 35.5 × 24.6 ; 2 ♂ 32.4 × 23.3, 41.9 × 28.5 mm (USNM). *Ibid.* 1 ♀ 32.6 × 22.6 ; 2 ♂ 38.2 × 27.4, 39.6 × 27.5 mm (QM). Tubai, Stn 349, 23°20.7′S, 149°31.9′W, trapped, 135 m, 5.12.1990 : 1 ♂ 30.1 × 20.9 mm (MNHN-B22238). Raevavae, Stn 346, 23°50.6′S, 147°42.5′W, trapped, 100 m, 3.12.1990 : 1 ♂ 34.2 × 23.9 mm (MNHN-B22233).

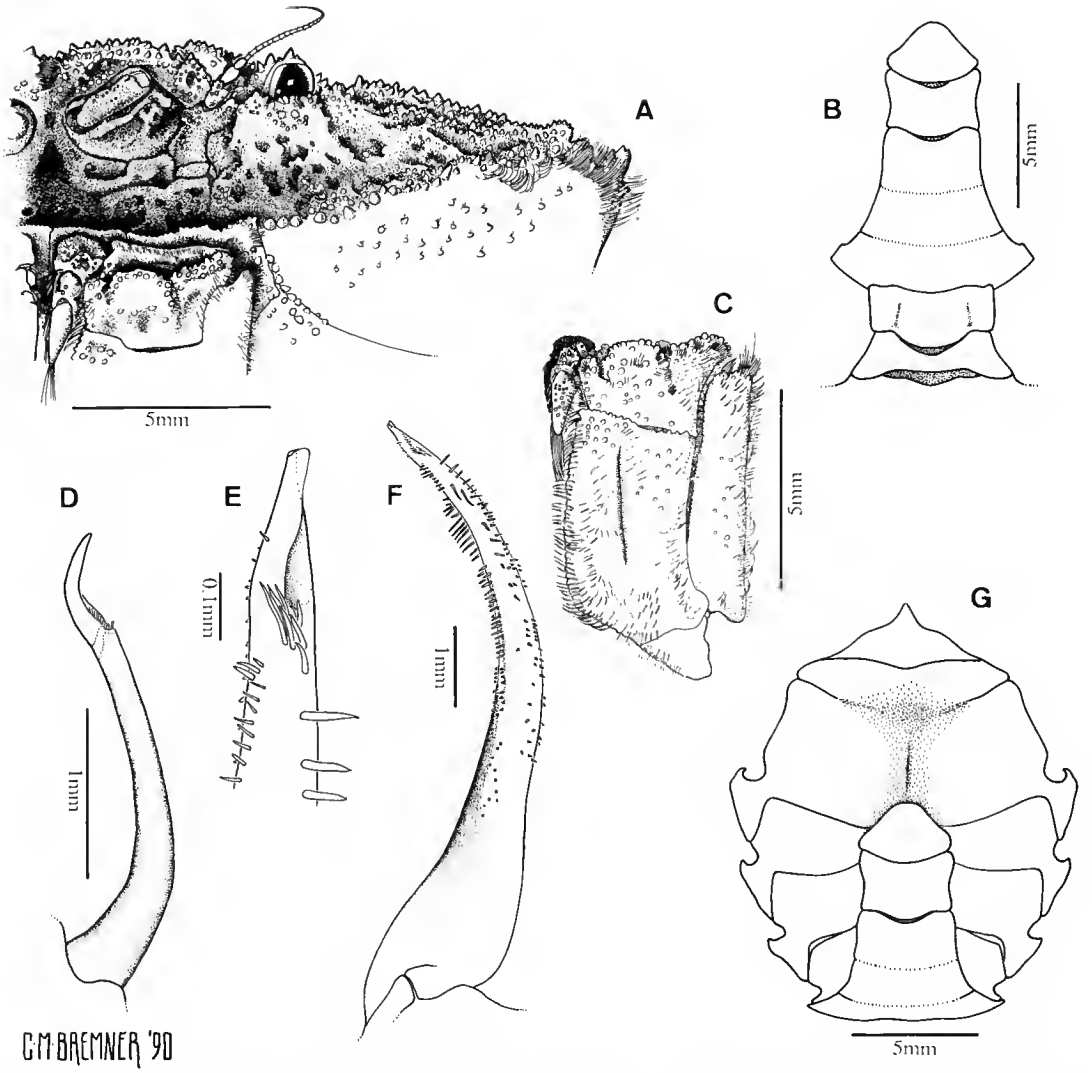

FIG. 7. — *Epistocavea mururoa* gen. nov., sp. nov. Holotype ♂, MNHN-B22235, Mururoa, Tuamotu Archipelago. A, frontal view; B, abdomen; C, third maxilliped; D, second gonopod; E, F, first gonopod; G, sternum and abdomen.

DESCRIPTION

Carapace transversely ovoid, *c.* 1.4-1.45 times broader than long. Fronto-orbital width *c.* 0.66-0.68 times carapace length. Carapace slightly convex in both directions, particularly over anterior third longitudinally. Regions moderately defined; 1F and 2F fused; 1M separated from 2F; 2M partially longitudinally divided, internal branch of 2M fused with 1M, outer

branch also partially divided anteriorly ; 2M separated from 3M ; 4M indistinct ; 1R and 2R fused, separated from 3R by shallow furrow ; 1P and 2P shallowly defined ; 2L and 3L fused. Anterolateral margins regularly convex ; slightly cristate ; divided into 4 teeth. Anterolateral teeth triangular, bluntly acute, second tooth the largest, followed by third ; first and fourth slightly smaller ; first tooth adjacent to lateral edge of orbit but well separated ; anterolateral margins continuing in an arc below orbit, meeting the anterolateral corner of the buccal frame, continuous with concave lower margin of epistome ; epistome projecting forward as a fine rim ; meri of third maxillipeds sharply angled to fit against epistome, thus completely sealing buccal cavity ; forming, with maxillipeds in place, a continuous convex arc with anterolateral margins ; whole region across front from below orbits deeply excavated, and surface markedly corrugated and pitted. Front *c.* 0.3 times carapace width ; *c.* 0.6 times fronto-orbital width ; moderately projecting, medially, with V-shaped medial notch, laterally oblique, slightly concave, lateral teeth blunt, slightly projecting ; pre-orbital granular shoulder ; lateral margins diverging posteriorly. Posterior margin *c.* 0.4 times carapace width. Carapace surface granulate, granules larger anteriorly, coalescing into irregular rows anterolaterally, especially below orbits. Setae short, covering entire surface. Upper orbital border evenly granular ; concave ; orbital fissures obsolete. Lower orbital border irregularly granular. Inner angle of lower orbital border formed by a triangular tooth. Antennal flagellum small and entering orbit ; flagellum very fine, reaching about half distance to lateral margin ; without accessory setae. Basal antennal segment broadly in contact with front ; granular ; with small outer lobe lying against inner tooth of orbit. Basal antennular segment triangular, excavated medially, flagellum folding obliquely. Inter-antennular septum narrow.

Third maxilliped : merus distinctly shorter than ischium ; merus wider than long ; upper third of merus sharply angled backwards, forming a concave shelf ; seen from antero-ventral position merus having antero-medial margin bilobed, with outer lobe produced laterally to form anterolateral angle. Ischium rectangular, *c.* 1.7 times longer than wide ; inner margin granular. Palp articulating at inner distal margin of merus ; carpus and propodus with small ridges and projections.

Chelipeds markedly unequal, right usually larger but sometimes left ; large and robust, smaller chela of similar form but less massive than large chela ; merus with posterior border bearing large granules ; otherwise surfaces covered with small granules, but margins unarmed ; carpus with a broad tooth at inner angle ; a tooth present on inner face of carpus slightly below inner angle ; outer margin granular, granules on upper surface coalescing to form deep corrugations and pits. Outer surface of palm sparsely granular, smooth ventrally, becoming progressively more granular towards dorsal margin ; upper surface with two longitudinal rows of fused granules connected to each other and to posterior margin by meshwork of short granular ridges ; inner proximal edge moderately produced as rounded lobe. Outer surface of palm naked. Inner surface of palm microscopically granular, with a few larger granules ventro-proximally. Immovable finger with ventral ridge ; moderately long. Length cutting edge *c.* 0.37-0.41 times length propodus (major chela). Ventral border of chela concave at base of fixed finger. Dorsal surface of dactyl smooth, rounded. Fingers pointed ; a narrow gape between cutting margins.

Walking legs of medium length ; flattened ; moderately slender ; second pair the longest, *c.* 1.25 times maximum carapace width. Merus of third leg *c.* 3.1-3.3 times as long as wide. Carpus *c.* 2.2-2.4 times as long as wide. Propodus *c.* 1.5-1.7 times as long as wide. Dactyli *c.*

1.7-1.8 times length of propodus. Dactyli stout, straight, and flattened ; terminating in an acute chitinous tip. Merus of anterior margin with a small sub-distal shoulder ; anterior margin unarmed terminally. Carpus with accessory carinae on upper surface. All segments generally smooth ; setae short, almost covering entire surface ; longer setae fringing margins.

Male abdomen relatively narrow ; five free segments ; third to fifth fused ; third segment the widest. First segment *c.* 0.75 times width third segment. Segments three-five tapering. Segment six *c.* 1.5-1.6 times wider than long. Telson *c.* 0.7 times longer than wide ; bluntly pointed.

Gonopods : G1 medium length ; slender ; curved. Setae present ; short ; arranged as on figure. G2 short ; evenly curved ; tip short, recurved.

Sternum relatively broad ; segments 3 and 4 fused, but suture line evident except medially.

Distribution. — Only known from French Polynesia, from the Society Islands, 16°26.5′S, 151°46.2′W, to the Austral Islands, 23°50.6′S, 147°42.5′W. Bathymetric range : 100-240 m.

Medaeus grandis sp. nov.

(Fig. 8 ; pl. 8)

Etymology. — Named in reference to its very large size compared to other known species of *Medaeus*.

Type material. — The large male 37.2 × 24.6 (MNHN-B22218) is designated as holotype. The other two specimens are paratypes.

Material examined. — **French Polynesia**. SMCB (J. Poupin) : **Tuamotu Archipelago** : Mururoa, 21°46.9′S, 138°55.4′W, trapped, 210 m, 30.11.1989 : 1 ♂ 37.2 × 24.6 mm (MNHN-B22218). *Ibid.* 1 ♂ 33.4 × 22.3 mm (MNHN-B22219). Hao, St 246, 18°04.5′S, 141°01.6′W, trapped, 90 m, 2.06.1990 : 1 ♀ 21.2 × 14.7 mm (MNHN-B22220).

Description

Carapace transversely ovoid ; *c.* 1.5 times broader than long (1.44 in female). Fronto-orbital width *c.* 0.7 times carapace length (0.76 in female). Carapace convex in both directions, especially longitudinally over anterior third, but only slightly from side to side. Regions well defined, elevated, separated by strong furrows ; 1F and 2F fused, slightly elevated ; 1M separated from 2M ; 2M completely divided longitudinally and outer lobe partially divided anteriorly ; 3M slightly bilobed posteriorly ; 4M very strongly elevated and separated from 3M ; all anterolateral regions defined, 2L divided into 3 equal-sized lobes, 5L and 6L divided in halves by horizontal and oblique furrows, respectively, 5L not completely ; 1R and 2R not separated, divided from 3R by a broad oblique furrow ; 1P with strongly elevated transverse ridge, only slightly narrower than posterior margin, with 2 very short, irregular granular crests above and below, slightly beyond its lateral edge ; 2P with a transverse granular row, elevated laterally, barely distinguishable medially ; posterior margin costate, with a raised granular rim ;

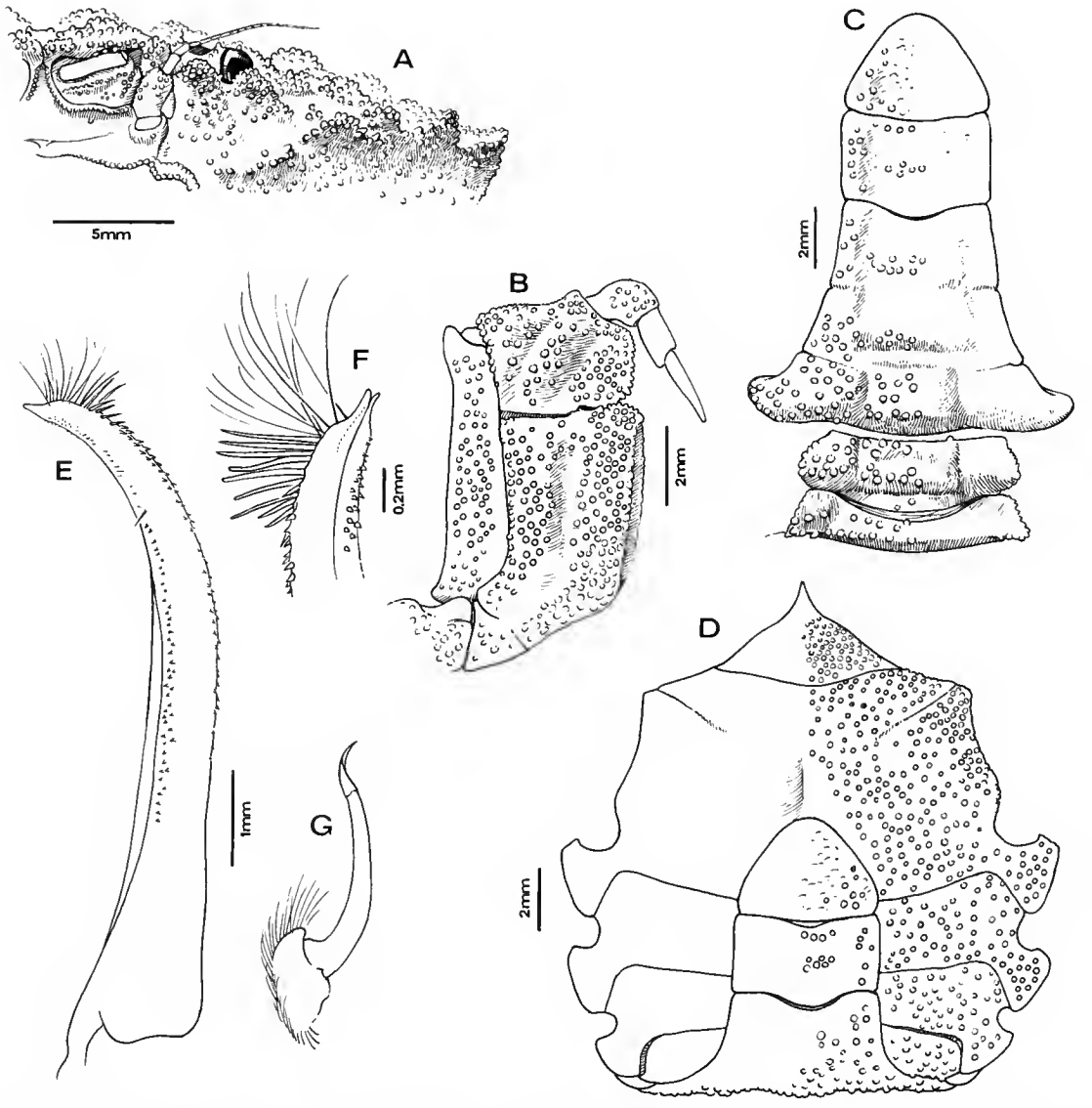

FIG. 8. — *Medaeus grandis* sp. nov. Holotype ♂, MNHN-B22218, Mururoa, Tuamotu Archipelago. A, frontal view ; B, third maxilliped ; C, abdomen ; D, sternum and abdomen ; E, F, first gonopod ; G, second gonopod.

posterolateral margins swollen and slightly convex at 1R/2R, then straight. Anterolateral margins regularly convex ; with five teeth behind the exorbital angle ; margins granular, first tooth the smallest, well separated from orbit, and situated lateral to, and well below, level of orbit seen in frontal view ; anterior to first tooth an ill-defined oblique granular row continuing

on towards anterolateral corner of buccal frame; second to fifth teeth increasing in size; second tooth relatively close to first tooth; all teeth triangular, bluntly pointed; greatest carapace width (across fifth teeth). Front *c.* 0.26-0.31 times carapace width; 0.7 times fronto-orbital width (0.76 on female); not deflexed and moderately projecting, granular; slightly more prominent, narrow medial projections separated by V-shaped notch; laterally receding, more-or-less straight; with more prominent blunt lateral projections; pre-orbital bluntly granular shoulder. Posterior margin *c.* 0.33-0.35 times carapace width (0.4 in female). Carapace surface granulate except in smooth furrows separating regions; almost entirely covered in very short setae which are lower than the granules. Upper orbital border concave, evenly granular; pair of shallow smooth furrows marking presence of broad truncate lateral tooth. Lower orbital border of inner angle formed by a triangular, granular, bluntly pointed tooth; laterally with a second smaller blunt granular lobe; with V-shaped notch laterally. Antennal flagellum small and entering orbit, fine, without accessory setae, reaching beyond orbit about half distance to first anterolateral tooth. Basal antennal segment broadly in contact with front, granular, rectangular, unarmed. Basal antennular segment with raised granular rim across upper and lateral margins, palp folding slightly obliquely. Inter-antennular septum moderately narrow, margins convex basally, outer edge of floor of antennular fossa, granular, more-or-less flat, slightly convex medially; lower margin of epistome projecting as thin rim.

Third maxilliped : merus distinctly shorter than ischium, width of merus *c.* 0.7 times length; antero-external angle produced, slightly rounded; *c.* 0.5 times length of ischium. Ischium sub-rectangular *c.* 1.7 times longer than wide.

Chelipeds markedly unequal; large and robust, left cheliped the larger on all present specimens; minor cheliped of similar form but with longer, more slender fingers. Merus with posterior border tuberculate; lower border granulate; anterior border tuberculate, slightly smaller tubercles than posterior border. Carpus with a broad tooth at inner angle; inner margin sharply granular; a tubercle with a row of sharp granules proximal to it present on inner face of carpus slightly below inner angle; outer margin granular and rugose. Outer surface of palm coarsely granular and coarsely rugose dorsally. Outer surface of palm without setae. Inner surface of palm granular. Immovable finger short (on major chela), with ventral ridge, and second longitudinal groove below cutting margin. Length of cutting edge *c.* 0.34 times length of propodus. Ventral border of chela slightly concave at base of fixed finger. Dorsal surface of dactyl minutely granular; dactyl very broad, bearing 3 longitudinal grooves on outer face, running most of length. Fingers pointed, recurved; cutting margins of both fingers with 3 large, molariform teeth over proximal two-thirds; without a noticeable gape between the cutting margins.

Walking legs of medium length; compressed; slender; first three pairs all of similar length, *c.* 1.1 times maximum carapace width. Merus of third leg *c.* 3.8-4.1 times as long as wide. Carpus *c.* 2.3-2.4 times as long as wide. Propodus *c.* 2-2.1 times as long as wide. Dactyli *c.* 1.3 times length of propodus. Dactyli slender, straight, and flattened; terminating in an acute chitinous tip. Merus of anterior margin terminating in a blunt tooth. Carpus with accessory carinae on upper surface. All segments granular, with a more prominent row of tubercles along upper margins of meri, and on antero-ventral borders, particularly of first two pairs; short setae cover entire surface, as on carapace, shorter than granules, longer on inside margins of dactyli.

Male abdomen relatively narrow ; five free segments ; third to fifth fused ; third segment the widest. First segment *c.* 0.75 times width third segment. Segments three-five tapering. Segment six not elongated, 1.7 times wider than long. Telson *c.* 0.7-0.75 times longer than wide ; evenly rounded.

Gonopods : G1 medium length, moderately stout, curved, tip finely pointed ; bearing row of long setae distally on dorsal margin behind apex. G2 moderately long, evenly curved, tip short, recurved.

Sternum relatively broad, granular, covered in very fine, very short setae.

DISTRIBUTION. — Known only from French Polynesia. Bathymetric range : 90-210 m.

REMARKS

This species belongs without doubt in *Medaeus* according to the modern diagnosis given by GUINOT (1967). Comparisons were also made with specimens of the other two species presently included in the genus — *Medaeus ornatus* Dana, 1852, and *M. elegans* A. Milne Edwards, 1867 — housed in the Muséum National d'Histoire Naturelle in Paris, and previously reported on by GUINOT (1967). *Medaeus ornatus* is much spinier than *M. grandis* and, in particular, the fourth anterolateral teeth are the most prominent and form the greatest carapace breadth ; the anterolateral teeth are also, in general, more upturned ; the median and lateral lobes of the front are much more projecting ; the margins of the leg segments are much spinier ; the dorsal surface of the palm of the cheliped has two rows of large granular lobes, and the dorsal margin of the dactyl has sharp tubercles. On *M. grandis* the palm of the chela lacks large lobules and the dactyl is only microscopically granular. There are also differences in male abdomen and pleopod shapes (GUINOT, 1967, fig. 39).

In general form *M. grandis* looks more like *M. elegans* but can be separated by having longer, slimmer legs ; a less medially protruding frontal margin ; a more granular carapace surface ; region 2L divided into three parts ; margins of each of the fused male abdominal segments 3-5 evenly tapering, not concave as in *M. elegans*, and by the shape of the male pleopod (GUINOT, 1967, fig. 38).

ACTAEINAE Alcock, 1898

MERACTAEA Serène, 1984

Meractaea Serène, 1984 : 103.

TYPE SPECIES. — *Meractaea brucei* Serène, 1984, by original designation.

DIAGNOSIS. — Carapace wider than long and transversely oval. Frontal border four-lobed with a rounded medial groove. Anterolateral borders of carapace regularly convex, bearing four teeth or lobes behind rounded exorbital lobe, tooth N being the largest. Dorsal surface of carapace longitudinally convex over anterior third but flattened from side to side ; completely lacking setae. Regions well separated by

smooth grooves bearing bulging granules of irregular size, some joined but most separated. Third maxilliped with bulging, rounded tubercle on outer medial face of merus. Chelipeds subequal ; same ornamentation as dorsal carapace regions. Fingers of chelipeds distally pointed ; crossing when closed. Walking legs narrow, smooth and naked except for some isolated long setae and rows of short setae on ventral borders of propodi and dactyli. First and second male pleopods are of same type as those of the Actaeinae. (Modified after SERÈNE, 1984.)

REMARKS

Meractaea Serène, 1984, has until now only contained the single species, *M. brucei* Serène, 1984, from Kenya, East Africa. The discovery of the present new species justifies its generic rank and marks it as a widespread Indo-West Pacific genus. The two species are remarkably similar, indeed, the presence of a large bulging tubercle on the outer face of the merus of the third maxilliped which was considered by SERÈNE (1984) to probably be a specific character, is also present on *Meractaea tafai* sp. nov. and I have therefore included it in the generic diagnosis.

Meractaea and *Rata* gen nov. (described later) are unique among the Actaeinae in having relatively long, slender walking legs. SERÈNE (1984) felt that only *Forestia* approached *Meractaea* in this regard, but even on *Forestia* the legs are closer to typical genera of Actaeinae than to either *Meractaea* or *Rata*. *Meractaea* is immediately identifiable by the characteristic pattern of carapace regions ; the bulging tubercles on carapace and pereiopods ; and the lack of dorsal carapace setae.

Meractaea tafai sp. nov.
(Fig. 9 ; pl. 9)

ETYMOLOGY. — Named in reference to a legendary Tahitian hero who was reputed to have red skin.

TYPE MATERIAL. — The larger male (23.9 × 15.7 mm) is designated holotype ; the other specimens are paratypes.

MATERIAL EXAMINED. — **French Polynesia**. SMCB (J.Poupin) : **Tuamotu Archipelago** : Stn 240, Acteons Maria, 22°01.8′S, 136°12.4′W, trapped, 150 m, 30.05.1990 : 1 ♂ 23.9 × 15.7 mm (MNHN-B22216). *Ibid.* 1 ♂ 14.0 × 9.0 mm ; 2 ♀ 32.0 × 21.0, 30.3 × 19.6 mm (MNHN-B22224).

DESCRIPTION

Carapace ovoid, *c.* 1.5-1.6 times broader than long. Fronto-orbital width *c.* 0.8 times carapace length. Carapace convex anteriorly, flat from side to side across postero-branchial regions. Regions distinct and well separated by narrow furrows, each taking the form of rounded bulges of various shapes, with uneven surfaces ; 1F and 2F fused, rising abruptly from just behind frontal margin ; 1M separated from 2F ; 1M separated from 2M ; 2M separated from 3M ; 2M longitudinally divided ; 3M divided basally into three parts, a narrow anterior projection and two basal rounded lobes ; 4M consisting of a row of 3 rounded tubercles, medial

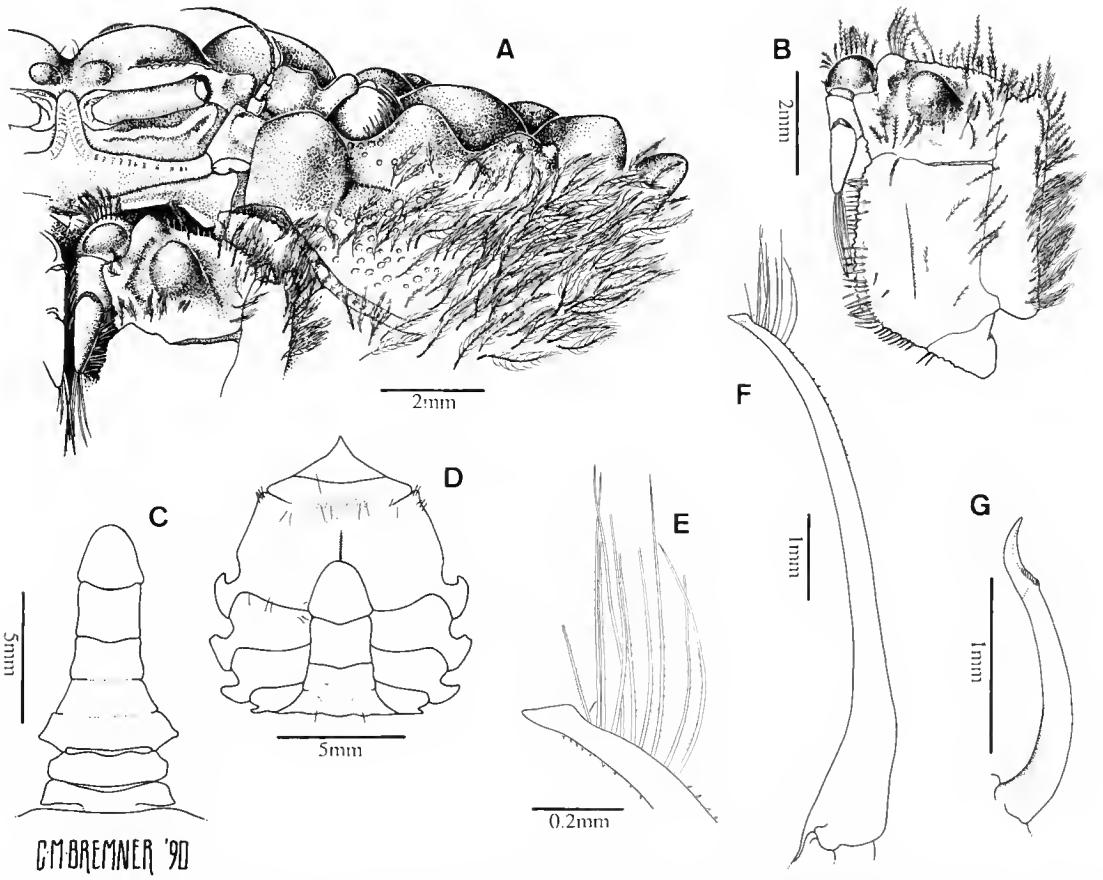

FIG. 9. — *Meractaea tafai* gen. nov., sp. nov. Holotype ♂, MNHN-B22216, Acteons Maria, Tuamotu Archipelago. A, frontal view ; B, third maxilliped ; C, abdomen ; D, sternum and abdomen ; E, F, first gonopod ; G, second gonopod.

one largest ; 1P divided longitudinally, with small rounded medial tubercle posteriorly ; 2P with two strong transverse crests, the anterior one divided medially ; postero-branchial regions with rounded granules and shallow furrows. Anterolateral margins regularly convex ; consisting of 5 evenly separated teeth including bluntly rounded orbital lobe ; second tooth much smaller, partially divided into 2 rounded granules ; third tooth longest, broad, bluntly pointed ; fourth tooth also large, narrower ; fifth tooth smaller, pointing postero-laterally. Front *c.* 0.3 times carapace width ; *c.* 0.55 times fronto-orbital width ; strongly sinuous, frontal margin with pair of narrow projecting, medial lobes and pair of equally projecting, but broad, lateral lobes ; lateral angles rounded, similarly projecting ; upper orbital border framed by three large rounded lobes, medial one smaller, lateral one equivalent to region 1L ; lower orbital border

concave medially, with large rounded inner lobe. Posterior margin *c.* 0.35 times carapace width. Antennal flagellum small and entering orbit. Basal antennal segment just touching front ; unarmed except for swollen, rounded medial tubercle. Basal antennular segment normal, flagellum folding almost transversely. Inter-antennular septum narrow.

Third maxilliped : merus distinctly shorter than ischium, *c.* 0.85 times wider than long, with a single large bulbous tubercle on outer face ; 0.6-0.65 times length of ischium. Ischium rectangular, *c.* 1.5 times longer than wide. Palp articulating at inner distal margin of merus.

Chelipeds subequal ; robust, moderately large ; height of palm *c.* 0.5 times length of palm including fixed finger. Merus with posterior border granulate ; with larger small, sharp granule subdistally ; armed with rounded tubercle terminally ; lower border granulate ; anterior border microscopically granular. Carpus with inner angle produced as a broad rounded tubercle ; upper surface of carpus covered with large, rounded, well-separated tubercles ; a tooth present on inner face of carpus slightly below inner angle. Outer surface of palm coarsely granular, granules arranged in 7 major rows ; uppermost two rows formed by very large, swollen, rounded tubercles as on carpus and carapace ; ventral two rows continuing onto fixed finger as strong, more-or-less smooth ridges, reaching to tip. Outer surface of palm naked. Inner surface of palm granular, with larger coarse granules medially ; bearing long setae below upper margin ; brown colouring of fixed finger extending proximally to about middle of palm as large rounded plume, on outer face colouring ending obliquely and not extending far onto palm. Length cutting edge *c.* 0.35 times length propodus. Ventral border of chela concave at base of fixed finger. Dorsal surface of dactyl microscopically granular ; with large bulbous tubercle basally. Fingers pointed ; without a noticeable gape between the cutting margins.

Walking legs relatively long ; flattened ; slender ; second pair the longest, *c.* 1.4 times maximum carapace width. Merus of third leg *c.* 3-3.2 times as long as wide. Carpus *c.* 2.5-2.6 times as long as wide. Propodus *c.* 2-2.1 times as long as wide. Dactyli *c.* 1.3-1.4 times length of propodus. Dactyli straight ; terminating in an acute chitinous recurved tip. Merus anterior margin unarmed terminally, upper margin armed with a row of small, semi-acute, distally pointing tubercles ; lower margin unarmed. Carpus with accessory carinae on upper surface. Upper margins of leg segments of carpus and propodus bearing row of larger blunt tubercles, appearing coarsely serrated ; otherwise surface of segments microscopically granular. Legs with scattered setae, and with fringe of very short setae on ventral margins of propodi and dactyli.

Male abdomen relatively narrow ; five free segments ; third to fifth fused. First segment broad, subequal in breadth to third. Segments three-five tapering. Segment six *c.* 1.1 times wider than long. Telson longer than sixth segment ; 0.95 times longer than wide ; evenly rounded.

Gonopods : G1 long, slender, curved ; long, feathered, setae present on distal dorsal margin. G2 short, evenly curved ; tip short, recurved.

Sternum relatively broad ; telson reaching *c.* half length of fused sternites 3 and 4 ; female abdomen relatively narrow, not covering sternum.

Colouration. — Furrows between regions, over anterior third of carapace, coloured dark reddish purple, becoming pale greenish blue posteriorly ; upper surfaces of bulbous regions orange. Upper surfaces of chelipeds coloured like carapace ; outer faces of palms becoming off-white ventrally. Each leg with an orange band proximally and distally on merus, and a medial band on carpus, propodus, and dactylus.

DISTRIBUTION. — Known only from the type locality in French Polynesia.

REMARKS. — *Meractaea tafai* sp. nov. is separable from the only other species in the genus, *M. brucei*, by several points. 1. The male first pleopod has the tip more truncated in *M. tafai*; and the setation also differs with *M. tafai* having more long feathered setae and lacking the short, more proximal bristles of *M. brucei*. 2. The dorsal carapace regions of *M. tafai* are even more strongly bulging and sharply defined, and although their surfaces are uneven, they are not granular as in *M. brucei*. 3. The upper margins of the meri of the walking legs are more coarsely granular in *M. tafai*.

RATA gen. nov.

ETYMOLOGY. — Named after a mythological Polynesian nautical hero, who was a grandson of Tafai. Gender is neuter.

TYPE SPECIES. — *Rata tuamotense* sp. nov., here designated.

DIAGNOSIS. — Carapace transversely ovoid, 1.4-1.5 times broader than long. Regions well defined. Anterolateral margins regularly convex; with four teeth behind the exorbital angle; a more-or-less distinct row of granules below first tooth running from second tooth to just short of lateral edge of orbit. Posterolateral margins convergent, not sharply defined, moderately cut-away to receive meri of last pair of legs. Front *c.* one-third carapace width; 0.5-0.6 times fronto-orbital width; not projecting, with a pair of broad lateral lobes and a pair of blunt tubercular projections medially. Upper orbital border concave; lower orbital border with inner angle formed by a triangular tooth, with V-shaped notch laterally. Antennal flagellum small and entering orbit; basal antennal segment just touching front. Basal antennular segment moderately broad, flagellum folds almost transversely, first segment of flagellum relatively slender and elongated. Inter-antennular septum moderately narrow, with a longitudinal furrow. Third maxilliped with merus distinctly shorter than ischium; merus wider than long, antero-external angle produced. Chelipeds subequal; large and robust; fingers pointed. Walking legs relatively long; compressed; moderately slender; dactyli slender and straight. Male abdomen relatively narrow; five free segments; third to fifth fused; first segment subequal in width to third, narrow. Gonopods: G1 long, slender, curved, reaching to suture between sternites 4 and 5; G2 short, evenly curved; tip short, reflexed, pointed.

REMARKS

Rata appears most closely related, amongst the Actaeinae, to *Forestia* Guinot, 1976. Only *Forestia* and *Meractaea* Serène, 1984, of all the Actaeinae genera, have the walking legs relatively elongated. *Meractaea* as discussed elsewhere in this paper is extremely unusual in many ways and not a close relative of *Forestia* or *Rata*. *Forestia* was originally erected to accept three species, *F. depressa* (White, 1847), *F. scabra* (Odhner, 1925) and *F. abrolhensis* (Montgomery, 1931). Subsequently, *F. pascua* Garth, 1985, has been described from Easter Island, but is known only from the single female type specimen.

Rata differs from *Forestia* in many characteristics.

1. The structure of the antennules and interantennular septum differ. In *Forestia* the first segment of the palp of the antennule is short and swollen and folds obliquely, whereas in *Rata* it is slender and elongated and folds almost transversely. The interantennular septum in *Forestia* is very narrow and sharp but in *Rata* it is noticeably wider and bears a vertical medial furrow.

2. The width of the front in *Forestia* (measured from the outer edge of the lateral teeth) is about one fourth of the carapace breadth. In *Rata* the frontal width is about one-third of the carapace breadth.

3. The frontal margin of *Forestia* is formed by two large convex lobes which are strongly produced and moderately depressed partly hiding the antennules in frontal view. In *Rata* the frontal margin is not at all produced, there is a small blunt tooth on either side of the medial line followed by slightly convex lateral lobes, and the antennules are not hidden in frontal view.

4. The walking legs in *Rata* are even more elongated and slender, and, in particular, the dactyli are very long and slender.

5. In *Forestia* the first segment of the male abdomen is relatively long, about the same length as segment 2, and flattened. In *Rata* the first segment is very narrow and not flattened.

6. In *Rata* the anteroexternal angle of the merus of the third maxilliped is strongly produced laterally, whereas in *Forestia* it is more nearly quadrate.

I have examined all the *Forestia* species except *F. pascua* (Garth). *F. pascua* appears somewhat different from the other three species and close to *Rata tuamotense* sp. nov. but unfortunately the description is not sufficient to be certain if it is really a true *Forestia*. The shape of the carapace, the wide, non-protruding front, the carapace regions and granulation, all strongly suggest the appearance of *Rata*. The antero-external angle of the third maxilliped is produced a little more than in typical *Forestia* species, but not as much as in *Rata tuamotense*. A careful examination of the frontal region is necessary to be sure of its correct generic placement. The two species can be easily separated because *F. pascua* has broader, more prominent anterolateral teeth, and the carapace region 2M is completely subdivided.

The differences between *Rata* and some of the genera of Xanthinae are not very great, and its placement in the Actaeinae is largely on subjective criteria, and on an assessment of its closest relatives. Guinot (1976) in an excellent study on the Actaeinae cleared up many problems but did not provide an assessment of the characters that are unique to the subfamily. A clear definition of the Actaeinae is still needed.

Rata tuamotense sp. nov.

(Fig. 10 ; pl. 10)

Etymology. — The name refers to the Island group in French Polynesia where the holotype was collected.

Type material. — The male of 20.9 × 14.5 mm (MNHN-B22231), from Fangataufa, is designated the holotype. All remaining material is paratypic.

Material examined. — **French Polynesia** SMCB (J. Poupin) : **Marquises Islands** : Tahuata, Stn 300, 9°54.5′S, 139°07.9′W, trapped, 190 m, 1.09.1990 : 1 ♀ 19.6 × 14.0 mm (USNM). — **Tuamotu Archipelago** : Tematangi, Stn 328, 21°40.6′S, 140°30.5′W, trapped, 270 m, 27.10.1990 : 1 ♂ 29.6 × 20.1 mm (MNHN-B22230). Fangataufa, Stn 231, 22°12.0′S, 138°45.9′W, trapped, 270 m, 21.05.1990 : 1 ♂ 20.9 × 14.5 mm (MNHN-B22231). Fangataufa, Stn 234, 22°15.0′S, 138°46.0′W, trapped, 250 m, 22.05.1990 : 1 ovig. ♀ 16.8 × 11.8 mm (MNHN-B22232)

DESCRIPTION

Carapace transversely ovoid, *c.* 1.4-1.47 times broader than long. Fronto-orbital width *c.* 0.82-0.86 times carapace length. Carapace convex anteriorly, flat from side to side across postero-branchial regions. Regions well defined, separated by broad, deep smooth grooves ; 1F and 2F not separated ; 1M distinct, anterior margin laterally oblique ; a small raised granular patch lateral to 1M and above middle of 2M ; 2M distinct, longitudinally divided for anterior three-quarters, with raised tubercle on either side of anterior end of dividing groove, outer branch much wider than inner branch ; 3M entire, anterior extension very narrow, reaching nearly to middle of 1M ; 4M distinct ; broad, smooth groove posterior to raised orbital rim ; 2L and 3L fused, armed with 3 or 4 larger granular tubercles ; 4L, 5L and 6L all distinct, armed with coarse tubercles of various size ; sub-parallel cardiac-intestinal grooves present, but cardiac region (1P) not clearly separated from 3R anterolaterally, and cardiac and intestinal regions not clearly separated from each other ; 2P with slightly raised, blunt ridges laterally above posterior margin. Anterolateral margins regularly convex ; with four teeth behind the exorbital angle ; first tooth in form of strong tubercle displaced slightly onto anterior surface ; below first tooth surface irregularly granular with a more-or-less distinct row of granules (of which one or two may form prominent tubercles) running from second tooth nearly to lateral edge of orbit, level with lower orbital margin ; second tooth broadly triangular, armed with accessory granules ; third tooth similar to second ; fourth similar but narrower ; carapace breadth slightly greater between third anterolateral teeth than fourth ; posterolateral margins convergent, not sharply defined, moderately cut-away to receive meri of last pair of legs. Front *c.* 0.3-0.33 times carapace width ; *c.* 0.52-0.56 times fronto-orbital width ; strongly sinuous in anterodorsal view ; in dorsal view not at all projecting, with a pair of broad lateral lobes and a pair of blunt tubercular projections medially ; lateral angles also moderately produced and armed with a few acute granules. Posterior margin *c.* 0.3 times carapace width in males ; 0.36 in females. Upper surface of carapace regions granular, granules unevenly sized, with larger, rounded tubercles laterally on regions 2L-5L ; each granule bearing semi-circlet of short stiff setae anteriorly ; setae thus forming a conspicuous covering. Upper orbital border evenly granular ; concave ; lateral fissures fused, evident as smooth grooves interrupting margin. Lower orbital border sinuous ; evenly granular ; inner angle formed by a triangular tooth ; with V-shaped notch laterally. Antennal flagellum small and entering orbit, fine, just reaching to outer edge of orbit. Basal antennal segment just touching front. Basal antennular segment moderately broad, flagellum folds almost transversely, first segment of flagellum relatively slender and elongated ; anterolateral margins of epistome granular, lower margin strongly projecting, sinuous, and deeply cleft. Inter-antennular septum moderately narrow, with a longitudinal furrow.

Third maxilliped : merus distinctly shorter than ischium ; merus wider than long, length *c.* 0.7 times width ; antero-external angle produced, rounded ; *c.* 0.6 times length of ischium. Ischium rectangular, length *c.* 1.4 times width.

Chelipeds subequal ; large and robust ; height of palm 0.55-0.6 times length including fixed finger. Merus with posterior border granulate, with broad subdistal lobe ; lower border minutely granulate, rounded ; anterior border minutely granulate. Carpus with inner angle produced, bluntly rounded ; connected by an oblique granular crest to a more-or-less produced, rounded, ventral tooth ; inner margin granular ; upper and outer surfaces covered

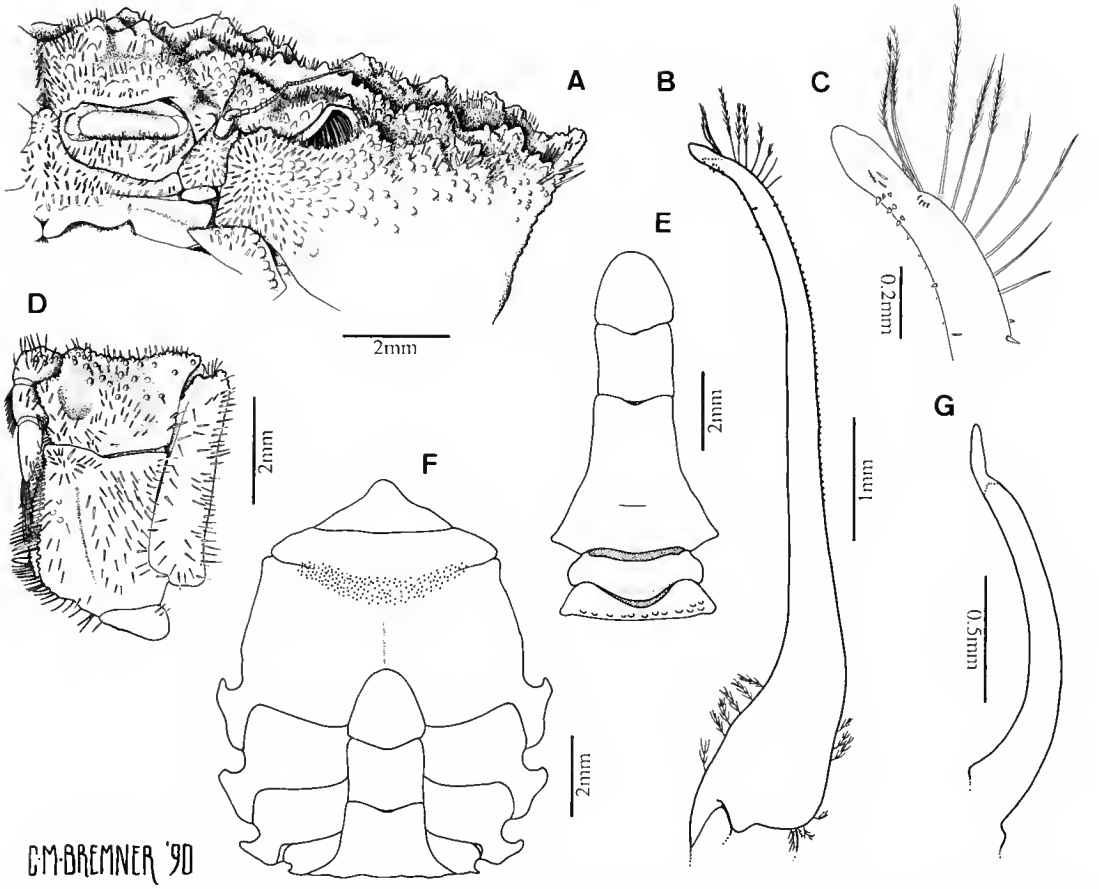

FIG. 10. — *Rata tuamotense* gen. nov., sp. nov. Holotype ♂, MNHN-B22231, Fangataufa, Tuamotu/Gambier Archipelago. A, frontal view ; B, C, first gonopod ; D, third maxilliped ; E, abdomen ; F, sternum and abdomen ; G, second gonopod.

in large, rounded, well-separated tubercles. Outer surface of palm coarsely granular, mostly arranged in 6-7 irregular rows ; densely covered by fine, stiff setae, not obscuring surface, longer on superior and inferior margins and around base of fingers. Inner surface of palm minutely granular on upper half ; more coarsely behind fixed finger. Immovable finger with ventral ridge ; moderately long ; length cutting edge *c.* 0.36 times length propodus. Ventral border of chela concave at base of fixed finger. Dorsal surface of dactyl granular. Fingers pointed ; without a noticeable gape between cutting margins.

Walking legs relatively long ; compressed ; moderately slender ; first three pairs of similar length ; *c.* 1.1 times maximum carapace width. Merus of third leg *c.* 2.7-2.8 times as long as wide. Carpus *c.* 2.2-2.3 times as long as wide. Propodus *c.* 1.7-1.8 times as long as wide. Dactyli *c.* 1.5-1.6 times length of propodus. Dactyli slender and straight ; terminating in an acute,

chitinous, recurved tip. Merus bearing small sharp granules along superior border ; a sub-distal tubercle ; terminating in an acute tooth ; blunt granules along inferior border. Carpus with a longitudinal sulcus on upper surface bordered by two rows of sharp tubercles. Propodus also with two rows of smaller, but relatively coarse, sharp tubercles. All segments covered with short setae, and fringed with longer stiff setae.

Male abdomen relatively narrow ; five free segments ; third to fifth fused ; first segment subequal in width to third, narrow. Segments three-five tapering. Segment six moderately elongated, *c.* 1.1 times wider than long. Telson about as long as wide ; triangular, rounded apically.

Gonopods : G1 long, reaching to suture between sternites 4 and 5 ; slender ; curved ; long, feathered setae on dorsal margin near tip ; small, conical setae along dorsal margin over distal half, and on ventral margin near tip ; tip hollowed ; gonopore subterminal ; bluntly pointed (as in figure) or more acute in large male. G2 short, evenly curved ; tip short, reflexed, pointed.

Colouration. — In life, background colour porcelain white with orange highlighting. Orange particularly strong : on frontal region and 1M ; towards anterior parts of other regions ; on anterolateral margins ; on distal border of carpus behind articulation with palm ; on superior inner margin of palm, and on the base of dactyl. Fingers blackened, but black colouration of fixed finger not extending backwards onto palm.

Distribution. — Known only from French Polynesia, between the Marquises Islands (9°54′S) and Tuamotu/Gambier Archipelago (22°15′S). Bathymetric range : 190-270 m.

Zosiminae Alcock, 1898

Lophozozymus bertonciniae Guinot and Richer de Forges, 1981 (Pl. 11)

Lophozozymus bertonciniae Guinot and Richer de Forges, 1981*a* : 1123-1127, fig. 2 A-D, pl. I, 5, 5a.

Material examined. — **French Polynesia**. SMCB (J. Poupin) : **Marquises Islands** : Tahuata, Stn 297, 9°54.3′S, 139°07.3′W, 100 m, trapped, 31.08.1990 : 1 ♀ 56.1 × 34.9, 1 ♂ 61.0 × 38.5 mm (MNHN). Hiva-Oa, 9°49.7′S, 139°09.1′W, 100 m, September 1989 : 2 ♀ 58.1 × 36.2, 60.0 × 37.1, 1 ♂ 64.7 × 41.0 mm (QM W8030). — **Tuamotu Archipelago** : Tenarunga, 21°21.0′S, 136°32.0′W, 160 m, trapped, 19.11.1989 : 1 ♀ 81.5 × 48.3 mm (MNHN). Mururoa, Stn 228, 21°51.9′S, 139°01.6′W, 200 m, trapped, 19.05.1990 : 1 ♀ 72.2 × 45.8, 1 ♂ 78.0 × 47.4 mm (USNM). — **Austral Islands** : Maria, Stn 420, 21°47.3′S, 154°42.4′W, trapped, 7.08.1991 : 1 ♀ 90.8 × 57.0 mm (MNHN). — **New Caledonia**. Collected by Mr. Barro : passe de Boulan, 200 m, 4.06.1978 : 1 ♂ 65.1 × 39.5 mm (MNHN).

Remarks

Lophozozymus bertonciniae Guinot and Richer de Forges, 1981, was well separated from most of its congenors as part of the original description. It seems that it is most closely related to *L. superbus* (Dana, 1852) and some confusion has persisted in separating the two species.

I have examined two specimens that can be attributed to *L. superbus*, one immature female (30.7 × 18.7 mm) in the MNHN previously mentioned by GUINOT (1977) from the type area (Tuamotu Arch.), and one larger male (40.7 × 24.8 mm) from Wreck Reef, southern Coral Sea, in the collections of the Queensland Museum. A neotype will need to be erected to firmly establish the identity of *L. superbus* as DANA's type specimen can be presumed destroyed as it has not been listed amongst DANA's surviving material. This action will be deferred awaiting additional material from the Tuamotus. Characters which can be used to separate the two species are given in the following. 1. The male abdomens differ in shape ; in *bertonciniae* the fused segments 3-5 have the sutures still quite strongly marked and the lateral borders of each original segment are produced laterally at their proximal ends ; whereas in *superbus* the sutures are hardly evident and the lateral margins are almost evenly tapering. 2. The inner lower orbital tooth in *bertonciniae* is somewhat flared outwards and projects strongly beyond the outer distal angle of the basal antennal segment, which is subquadrate ; in *superbus*, the inner lower orbital tooth is not flared outwards and does not project very far past the outer distal angle of the basal antennal segment, which itself is markedly produced and lies against the inner orbital tooth. 3. In *bertonciniae* the first anterolateral tooth is sharply cristate, and obliquely projecting upwards, with its ventral surface flat ; in *superbus*, the tooth is slightly deflexed ventrally, with its edge rolled in such a way that it overhangs and forms a groove below it. These differences also apply in less marked degree to the second anterolateral tooth. 4. In *superbus* the dorsal carapace surface is evenly covered with many punctations, each with a small tuft of short setae ; in *bertonciniae* the upper surfaces of the regions mostly lack punctations, and are smooth and glabrous.

Lophozozymus superbus is apparently a shallow water coral reef species, but *L. bertonciniae* seems to prefer deeper water with all records between 100 and 200 m.

DISTRIBUTION. — Southern Pacific Ocean, from New Caledonia (type locality) to French Polynesia. These records mark a major range extension. Bathymetric range : 100-200 m.

LIOMERINAE Sakai, 1976

MERIOLA gen. nov.

ETYMOLOGY. — Formed by re-arranging the letters of *Liomera*. Gender is feminine.

TYPE SPECIES. — *Meriola rufomaculata* sp. nov., here designated.

DIAGNOSIS. — Carapace transversely ovoid ; *c.* 1.5-1.6 times broader than long. Regions moderately defined ; orbital margin swollen. Anterolateral margins regularly convex ; with four teeth behind the exorbital angle ; margins bluntly crested. Front *c.* one-quarter carapace width ; moderately projecting ; bilobed ; lateral angles bluntly prominent. Posterior margin *c.* 0.4 times carapace width. Upper orbital border concave. Basal antennal segment just touching front ; flagellum small and entering orbit. Basal antennular segment moderately broad, palp folding almost transversely. Inter-antennular septum narrow. Merus of third maxilliped wider than long, distinctly shorter than ischium. Chelipeds large and robust ; ventral border of chela concave at base of fixed finger ; fingers spooned ; a narrow gape between cutting

margins on male. Walking legs relatively long; compressed; slender; all four pairs of similar length, dactyli straight and flattened; terminating in an acute, chitinous tip; anterior margin of merus unarmed terminally. Male abdomen of five free segments; third to fifth fused. Male first gonopod long, moderately stout, curved; tip shaped like " swans head ". Long setae present on dorsal margin and continuing along lower edge of hollowed tip. Sternum relatively broad.

Remarks

Meriola is considered here to contain two species, the type *M. rufomaculata* sp. nov., and *M. acutidens* (Sakai, 1969). *M. acutidens* was originally described as a *Neoliomera* by Sakai, but was clearly aberrant within that genus. Serène (1977) transfered it to *Liomera* (*Bruciana*), his new subgenus, as it seemed to him most closely related to *Liomera pediger* Alcock, 1898, which he had made the type for *Bruciana*.

The specimens of *Liomera* (*Bruciana*) *pediger* at the MNHN, Paris, identified by Serène, were compared with *Meriola rufomaculata*, and they are clearly not congeneric. I, like Serène, have also not examined material of Sakai's *acutidens*, but the similarities between it and the present new species are striking. These include the shape and long length of the walking legs; the degree and pattern of regionation; and the shape of the carapace which has relatively very long posterolateral margins that are not as sharply oblique as is typical of *Liomera* and *Neoliomera*. Within *Liomera* and *Neoliomera* the pattern of regions and their degree of development varies considerably, but the very long, thin legs and the shape of the carapace are more than enough to exclude the species here placed into *Meriola*.

The subgenus *Bruciana* as characterised by *Liomera* (*Bruciana*) *pediger* is of a much more typical *Liomera* appearance. It differs from *Meriola* in a number of features: 1, the carapace regions are all strongly and clearly defined; 2, the walking legs, while being longer than a typical *Liomera*, are still quite short, have the meri convex, and are quite different from the very long, slender legs of *Meriola*; 3, the first anterolateral tooth is clearly marked and separate from the orbit; 4, the shape of the epistome, antennae and antennules is different. In *L. pediger* the basal segment of the antenna is relatively elongated and lies very obliquely (*c.* 45°), forming the outer half of the floor of the antennular fossa; and in conjunction with this the epistome is unusually narrow. The basal antennal segment of *Meriola rufomaculata* is more usual in form, being quite short and only slightly oblique, so that the epistome forms most of the floor of the antennular fossa (compare figs 11 A and 11 I).

The taxonomic position of *Meriola* is not completely clear. It largely satisfies the definition of the Liomerinae given in the key of Serène (1984) although none of the characters is exclusively definitive for the subfamily. In its general shape and conformation of the front it shows similarities with some members of the Xanthinae, in particular *Xanthias*, but the ungulate tips of the fingers exclude it from almost all genera of Xanthinae except for *Leptodius* and *Macromedaeus*, neither of which it resembles at all. Until a more rigorous examination of subfamilial relationships is undertaken it is placed in the Liomerinae.

Meriola rufomaculata sp. nov.
(Fig. 11A-H ; pl. 12)

ETYMOLOGY. — The name refers to the pattern of large red patches on the dorsal surface of the carapace.

TYPE MATERIAL. — The male is designated the holotype, and the female a paratype.

MATERIAL EXAMINED. — **French Polynesia**. SMCB (J. POUPIN) : **Tuamotu Archipelago** : Vanavana, Stn 331, 20°45.7'S, 139°10.1'W, trapped, 240 m, 28.10.1990 : 1 ♂ 32.0 × 20.4 mm (MNHN-B22223). Fangataufa, Stn 231, 22°12.0'S, 138°45.9'W, trapped, 270 m, 21.05.1990 : 1 ♀ 31.8 × 20.3 mm (MNHN-B22222)

DESCRIPTION

Carapace transversely ovoid ; *c.* 1.57 times broader than long. Fronto-orbital width *c.* 0.7 times carapace length. Carapace evenly convex longitudinally, flat from side to side. Regions moderately defined ; 1F marked by swollen rounded ridge parallel to frontal margin ; 2F not distinct ; 1M moderately swollen and separated by broad, shallow groove from inner branch of 2M ; 2M partially longitudinally divided anteriorly by broad, shallow groove, outer branch of 2M wider than inner branch ; 2M separated from 3M ; orbital margin swollen and separated from posterior regions by strong groove ; 1L, 2L and 3L fused, delimited posteriorly by strong, oblique, slightly concave groove originating on lateral margin between second and third anterolateral teeth ; a similar, much shorter groove between third and fourth teeth ; cardiac and intestinal regions defined by diffused grooves. Anterolateral margins regularly convex ; with four teeth behind the exorbital angle ; margins bluntly crested ; first tooth lateral to orbit, well separated, connected by straight, slightly oblique margin very poorly defined in frontal view ; ill defined, granular, slightly flattened area running from first tooth obliquely below orbit ; second tooth broad, rounded ; third tooth narrower, slightly more prominent, blunt ; fourth tooth similar to third but smaller ; carapace width between fourth teeth slightly more than, or subequal to, distance between third teeth. Front *c.* 0.26 times carapace width ; *c.* 0.57-0.58 times fronto-orbital width ; moderately projecting ; bilobed ; lateral angles bluntly prominent ; pre-orbital teeth represented as blunt shoulder. Posterior margin *c.* 0.37-0.4 times carapace width. Carapace surface smooth and shining, finely punctate, finely wrinkled and roughened anteriorly ; without setae. Upper orbital border concave, smooth, granular laterally. Lower orbital border granular laterally ; inner angle formed by a rounded lobe. Antennal flagellum small and entering orbit, not reaching beyond orbit. Basal antennal segment just touching front. Basal antennular segment moderately broad, palp folds almost transversely. Inter-antennular septum narrow.

Third maxilliped : merus distinctly shorter than ischium, wider than long, length *c.* 0.7-0.8 times breadth ; *c.* 0.4 times length of ischium. Ischium rectangular, length *c.* 1.6 times breadth ; inner margin smooth.

Chelipeds markedly unequal on male holotype, but subequal on female paratype (probably regenerating) ; large and robust ; merus with posterior border granulate ; lower border

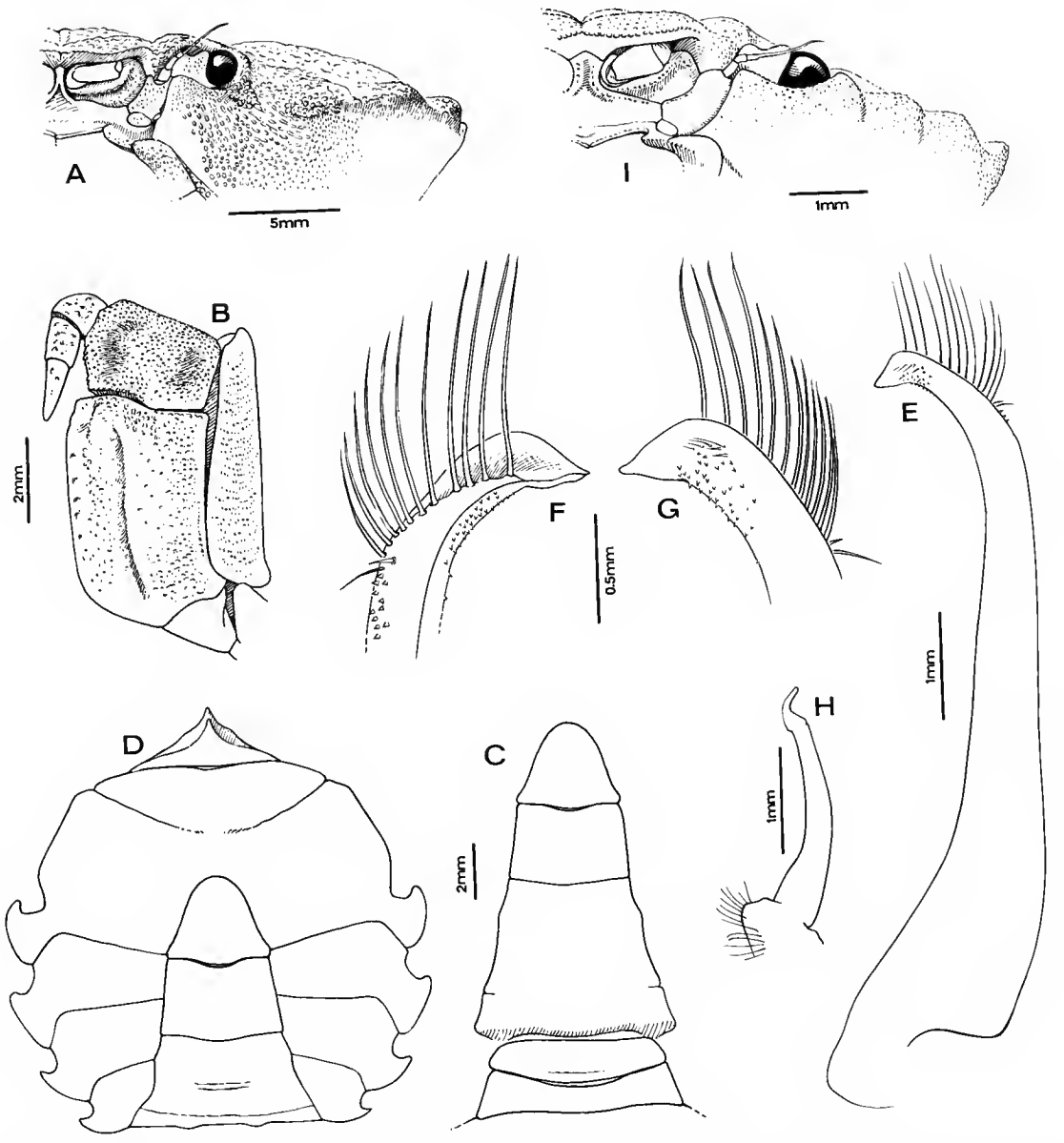

FIG. 11. — A-H, *Meriola rufomaculata* gen. nov., sp. nov. Paratype ♀, MNHN-B22222, Fangataufa, Tuamotu/Gambier Archipelago. A, frontal view ; B, third maxilliped ; C, abdomen ; D, sternum and abdomen ; E, F, G, first gonopod ; H, second gonopod. I, *Liomera* (*Bruciana*) *pediger* (Alcock, 1898) : frontal view.

granulate ; anterior border minutely granulate ; carpus with two bluntly rounded teeth at inner angle ; outer margin and upper surface smooth, finely punctate. Outer surface of palm appearing smooth, but microscopically granular and punctate ; without setae. Inner surface of palm microscopically granular. Immovable finger moderately long, with ventral ridge extending a short distance on palm ; length of cutting edge *c.* 0.32-0.36 times length of propodus. Ventral border of chela concave at base of fixed finger. Dorsal surface of dactyl smooth, rounded. Fingers spooned ; a narrow gape between cutting margins on male.

Walking legs relatively long ; compressed ; slender ; all four pairs of similar length, *c.* 1.2 times maximum carapace width. Merus of third leg *c.* 4.2 times as long as wide. Carpus *c.* 2.4 times as long as wide. Propodus *c.* 2.5-2.6 times as long as wide. Dactyli *c.* 1.3 times length of propodus. Dactyli straight and flattened ; terminating in an acute chitinous tip. Merus anterior margin unarmed terminally. Carpus without accessory carinae on upper surface, but sometimes with slight distal depression. All segments smooth ; without setae.

Male abdomen : five free segments ; third to fifth fused ; first and third segments subequal in width. Segments three-five tapering. Segment six *c.* 1.5 times wider than long. Telson *c.* 0.9 times longer than wide ; evenly rounded, slightly longer than segment 6.

Gonopods : G1 long ; moderately stout ; curved ; tip shaped like " swans head ". Long setae present on dorsal margin and continuing along lower edge of hollowed tip. G2 short ; evenly curved ; tip short.

Sternum relatively broad, smooth, noticeably punctate.

Colouration. — Male specimen strongly marked with large, symmetrical orange/red patches on the dorsal surface of carapace on the following regions : on 1F-1M ; on outer half of 2M ; anterolaterally on 1L-3L ; small patch on 4L ; on 5L ; on 3M ; round patch on cardiac ; and a round patch posterolaterally above bases of last walking legs. Legs with sub-proximal and sub-distal bands on meri, and a single band more-or-less medially on other segments. Base colour of carapace (after preservation) is a light blue-gray ; legs creamy yellow. Fingers dark, as usual, with the colour of fixed finger extending obliquely backwards a short distance onto the palm.

Incertae sedis

EURYOZIUS Miers, 1886

Pseudozius (*Euryozius*) Miers, 1886 : 141-142.
Euryozius ; Guinot, 1968*b* : 325-330.
Gardineria Rathbun, 1911 : 236. Guinot, 1968*b* : 325-330.

Type species. — *Pseudozius bouvieri* A Milne Edwards, 1869.

Diagnosis. — Carapace transversely oval ; anterolateral margin directed obliquely downward to the angle of the buccal cavity and furnished with a stridulating mechanism. Orbit sub-entire, pear-shaped. Antennules large, nearly transverse. Peduncular segments of antennae narrow ; basal segment falling far

short of front, following segment just touching front ; flagellum standing in orbital hiatus. Efferent ridge well developed posteriorly but not reaching anterior edge of buccal cavity. Merus of maxillipeds expanded at outer angle. Chelipeds stout, smooth. Legs slender, flattened (after RATHBUN, 1911).

REMARKS. — GUINOT (1968*b*) discussed the relationships of *Gardineria* and *Euryozius* Miers, 1886, at some length. At that time she elected to maintain them as separate genera because, even though they are clearly closely allied, *G. canora* is only known from a single female and she felt the structure of the male pleopods may be important in determining their true status. CROSNIER (in SERÈNE, 1984) put *Gardineria* into the synonymy of *Euryozius* by placing *G. canora* into *Euryozius*. After examining specimens of *Euryozius bouvieri* at the MNHN I concur with CROSNIER's action.

Euryozius is now considered to have three species : *E. bouvieri* (A. Milne Edwards, 1868) from the Western Atlantic ; *E. canorus* (Rathbun, 1911) from the Seychelles, in the Indian Ocean ; and *E. danielae* sp. nov. from French Polynesia, in the Pacific Ocean. The latter two are known only from single females.

Euryozius danielae sp. nov.

(Fig. 12 ; pl. 13)

ETYMOLOGY. — This elegant crab is named in honour of Dr Danièle GUINOT of the MNHN Paris, for her work on resolving the problems of this group.

MATERIAL EXAMINED. — **French Polynesia**. SMCB (J. POUPIN) : **Society Islands** : Maupiti, Stn 272, 16°25.6'S, 152°17.5'W, trapped, 110 m, 24.06.1990 : 1 ♀ 26.7 × 16.3 mm (holotype, MNHN-B22217)

DESCRIPTION

Carapace transversely ovoid ; *c.* 1.65 times broader than long. Fronto-orbital width *c.* 0.9 times carapace length. Carapace convex anteriorly, flat from side to side. Regions poorly defined ; cardiac indistinct ; intestinal indistinct, defined laterally by branchio-intestinal grooves. Anterolateral margins regularly convex ; cristate, slightly raised, appearing granular from above ; ending posteriorly in 2 projecting, spinous teeth, first forming widest point of carapace, second with short oblique inwardly directed ridge. Anterolateral margins not connected with outer edge of orbit ; ventral edge of margins finely striated, forming a long stridulatory ridge, anteriorly curving beneath orbit but stopping clearly short of anterolateral corner of buccal frame. Front *c.* 0.25 times carapace width ; *c.* 0.45 times fronto-orbital width ; moderately deflexed ; bilobed with deep median incision ; lateral angles rounded, projecting ; lateral margins diverging posteriorly. Posterior margin *c.* 0.25 times carapace width. Carapace surface smooth, shining, punctate, surface coarsened with fine punctations in band across front and behind anterolateral margins ; without setae. Upper orbital border irregularly granular laterally ; concave ; inner angle rounded. Lower orbital border irregularly granular, outer edge of orbit marked by a single prominent tubercle ; a second, similar, below middle of cornea, then 3-4 tubercles along inner part. Antennal flagellum small, entering orbit, reaching just short of end of cornea. Orbital hiatus open. Basal antennal segment short, not touching front ;

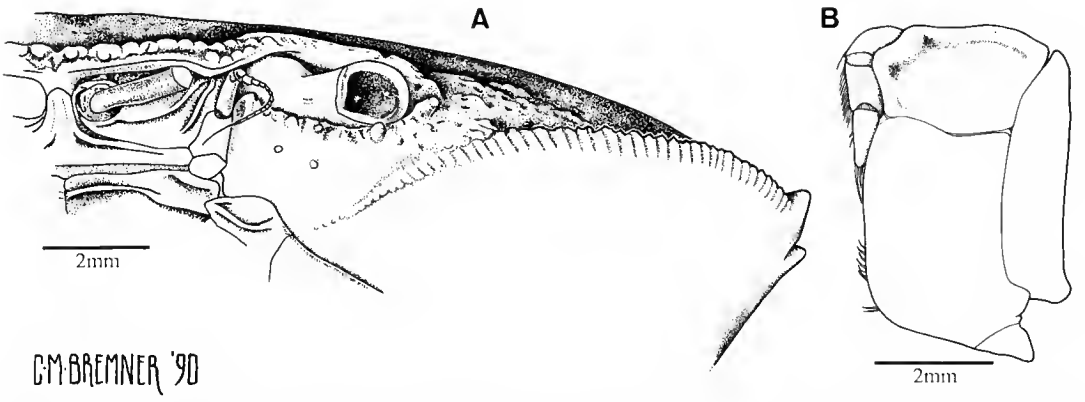

FIG. 12. — *Euryozius danielae* sp. nov. Holotype ♀, MNHN-B22217, Maupiti, Society Islands. A, frontal view ; B, third maxilliped.

unarmed ; subrectangular. Basal antennular segment triangular, with anterior and lateral edges raised to form a rim ; palp folding obliquely. Inter-antennular septum narrow.

Third maxilliped : merus distinctly smaller than ischium ; *c.* 0.6 times wider than long ; antero-external angle produced, rounded ; *c.* 0.5 times length of ischium. Ischium sub-triangular, *c.* 1.6 times longer than wide ; inner margin smooth, upper surface punctate. Maxillipeds without fringing setae. Palp articulating at inner distal margin of merus.

Chelipeds large and robust ; markedly unequal, left the larger on present specimen (ratios for major cheliped) ; height of palm *c.* 0.5 times length, palm relatively elongated with dactyl *c.* 1.2 times length of superior margin. Merus with posterior border smooth, bearing small subdistal lobe, produced medially as strong rounded triangular lobe ; lower border smooth, evenly rounded without a border marked ; anterior border smooth, with small, blunt, ischio-meral tooth basally. Carpus with broad tooth at inner angle, inner margin produced as a long, microscopically granular crest that rubs against the stridulatory crest on the carapace ; outer margin smooth. Outer surface of palm smooth and punctate especially dorsally. Outer surface of palm naked. Inner surface of palm smooth. Immovable finger moderately long ; rounded on outer surface ; with low ventral ridge and with a series of spaced punctations in furrow, extending posteriorly to level of insertion of dactyl. Length cutting edge *c.* 0.4 times length propodus. Ventral border of chela straight. Dorsal surface of dactyl smooth, rounded. Fingers pointed, crossing ; without a noticeable gape between the cutting margins

Walking legs relatively long ; flattened ; slender ; third pair the longest, *c.* 1.25 times maximum carapace width. Merus of third leg *c.* 4.5 times as long as wide. Carpus *c.* 2.7 times as long as wide. Propodus *c.* 4.1 times as long as wide. Dactyli longer than propodi ; slender, straight, and flattened ; terminating in an acute chitinous recurved tip. Anterior margin of merus with a sub-distal shoulder ; anterior margin unarmed terminally. Carpus without accessory carinae on upper surface. All segments smooth ; naked except for a few fine setae on margins, particularly on inner edge of dactyli.

Sternum and abdomen : Sternum relatively broad. Female abdomen relatively narrow, not covering sternum ; telson large and triangular, much longer than other segments.

REMARKS. — *Euryozius danielae* sp. nov. is separable from *E. canorus* (Rathbun) in the following respects : 1, the width to length ratio is markedly different (1.65 in *danielae*, 1.45 in *canorus*) ; 2, the two lateral teeth are much more prominent and projecting in *danielae* ; 3, the fingers of the chelipeds are almost entirely coloured black in *danielae*, but coloured like the palm and only darkening distally in *canorus* ; 4, the frontal margin is not as strongly deflexed as it is in *canorus*, and can be seen from above ; in particular the median incision is marked and easily observed in *danielae*. Both the above species are easily separable from *E. bouvieri* (A. Milne Edwards, 1869) by having the meri of the walking legs noticeably longer and more slender.

DISTRIBUTION. — Known only from the type locality in Society Islands in French Polynesia, from a depth of 110 m.

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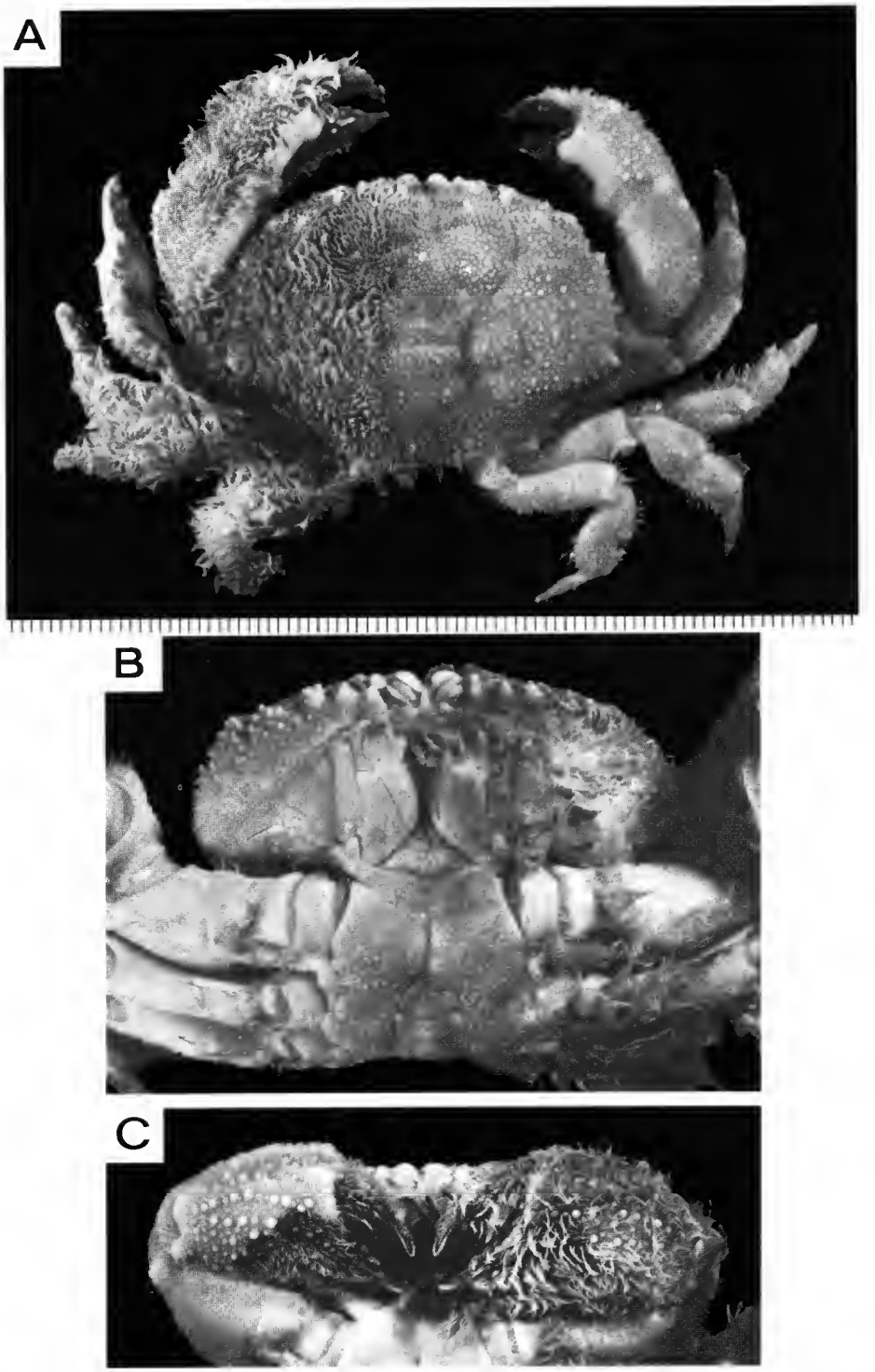

PLATE 1. — *Banareia fatuhiva* sp. nov. Holotype ♂, MNHN-B22228, Tahuata, Marquises Islands. A, dorsal view ; B, ventral view ; C, frontal view, showing chelipeds. Specimen partially denuded. Scale in mm.

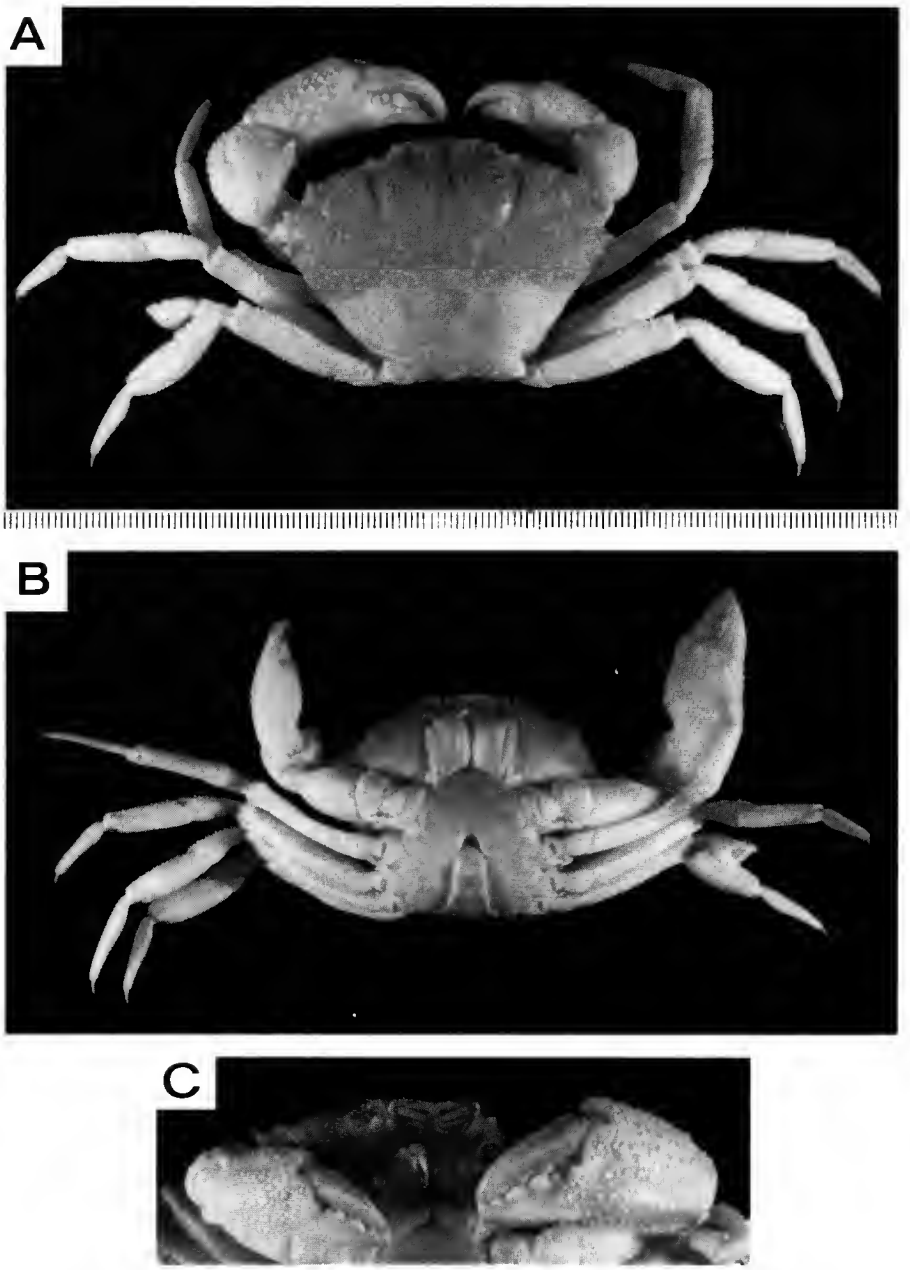

PLATE 2. — *Demania garthi* Guinot and Richer de Forges, 1981. ♂, MNHN-Unreg., Mururoa, Tuamotu Archipelago, 30.11.1989. A, dorsal view ; B, ventral view ; C, frontal view, showing chelipeds. Scale in mm.

PLATE 3. — *Demania mortenseni* (Odhner, 1925). ♂, MNHN-B22248, Akiaki, Tuamotu Archipelago. A, dorsal view ; B, ventral view ; C, frontal view, showing chelipeds. Scale in mm.

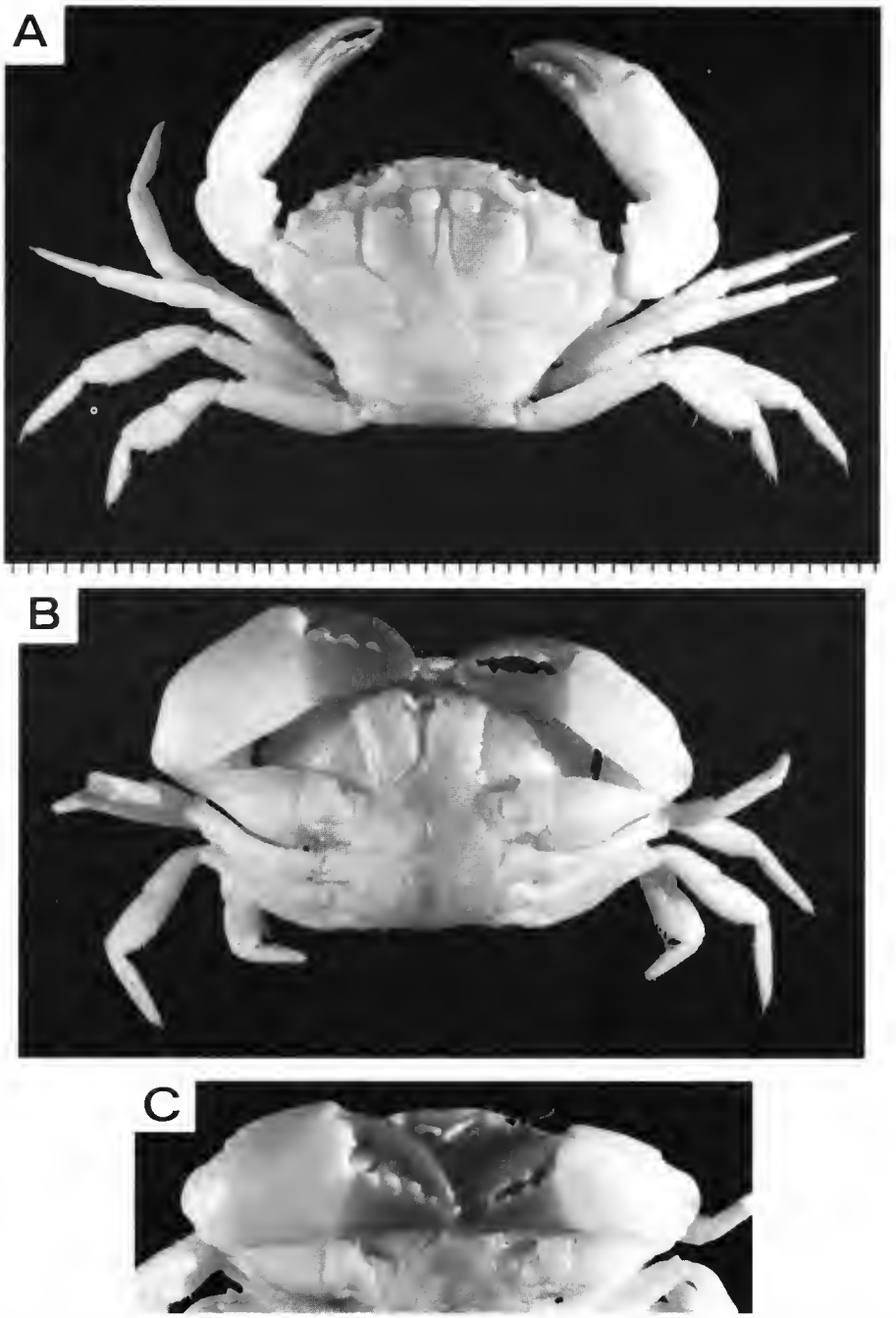

PLATE 4. — *Paraxanthodes polynesiensis* sp. nov. Holotype ♂, MNHN-B22225, Mururoa, Tuamotu Archipelago. A, dorsal view ; B, ventral view ; C, frontal view, showing chelipeds. Scale in mm.

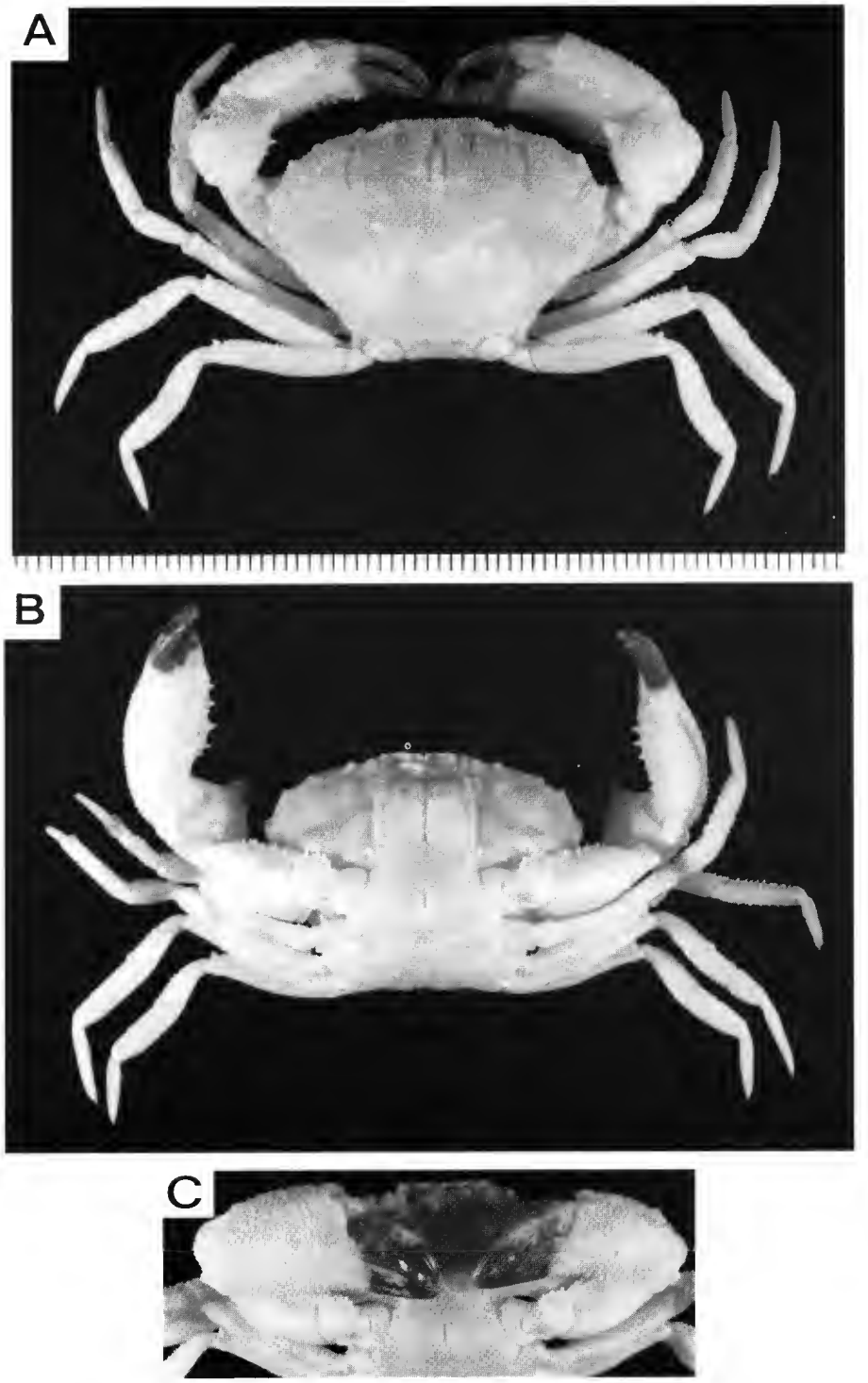

PLATE 5. — *Alainodaeus akiaki* gen. nov., sp. nov. Holotype ♂, MNHN-B22243, Rurutu, Austral Islands. A, dorsal view ; B, ventral view ; C, frontal view, showing chelipeds. Scale in mm.

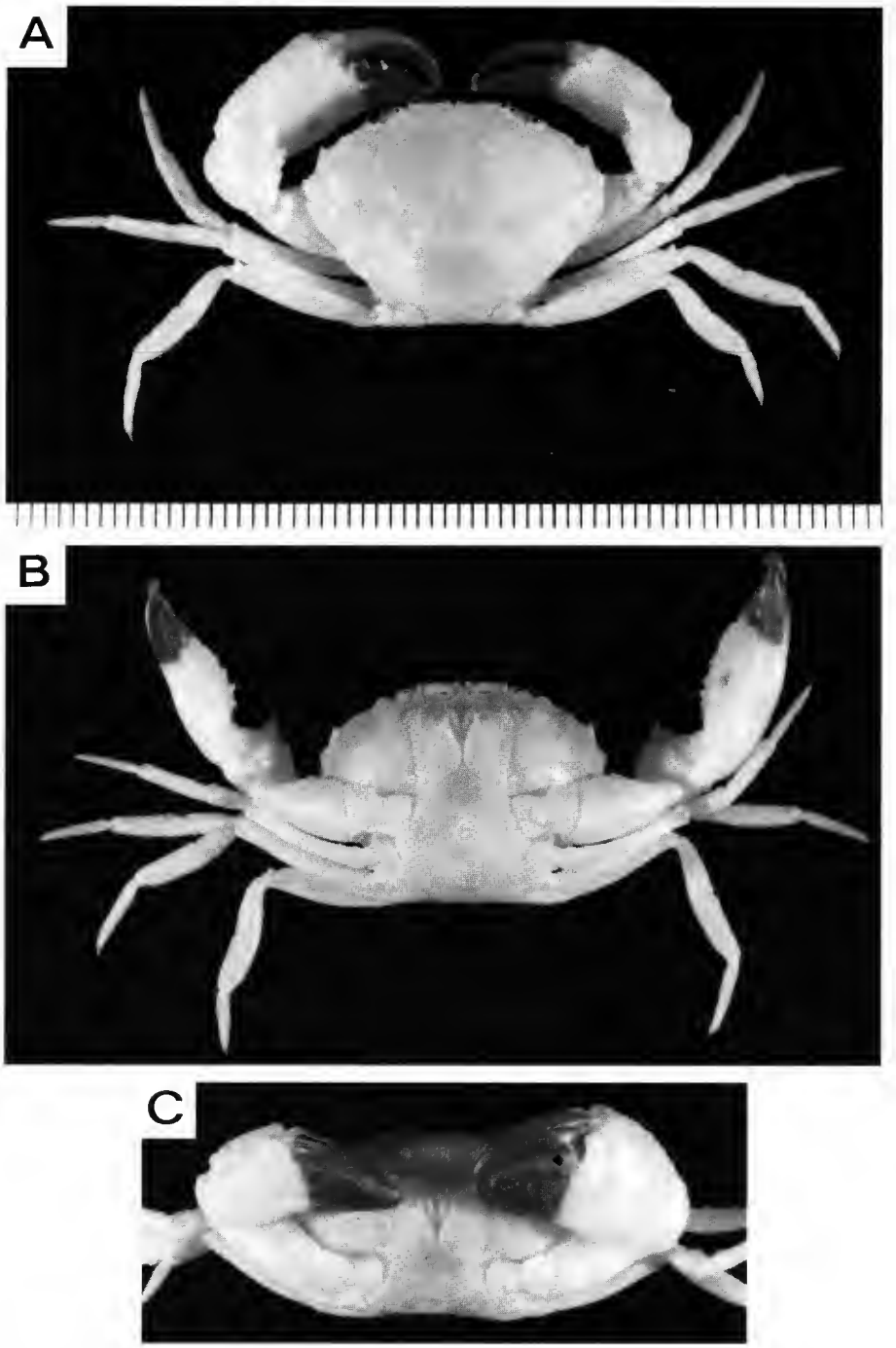

PLATE 6. — *Alainodaeus rimatara* gen. nov., sp. nov. Holotype ♂, MNHN-B22244, Akiaki, Tuamotu Archipelago. A, dorsal view ; B, ventral view ; C, frontal view, showing chelipeds. Scale in mm.

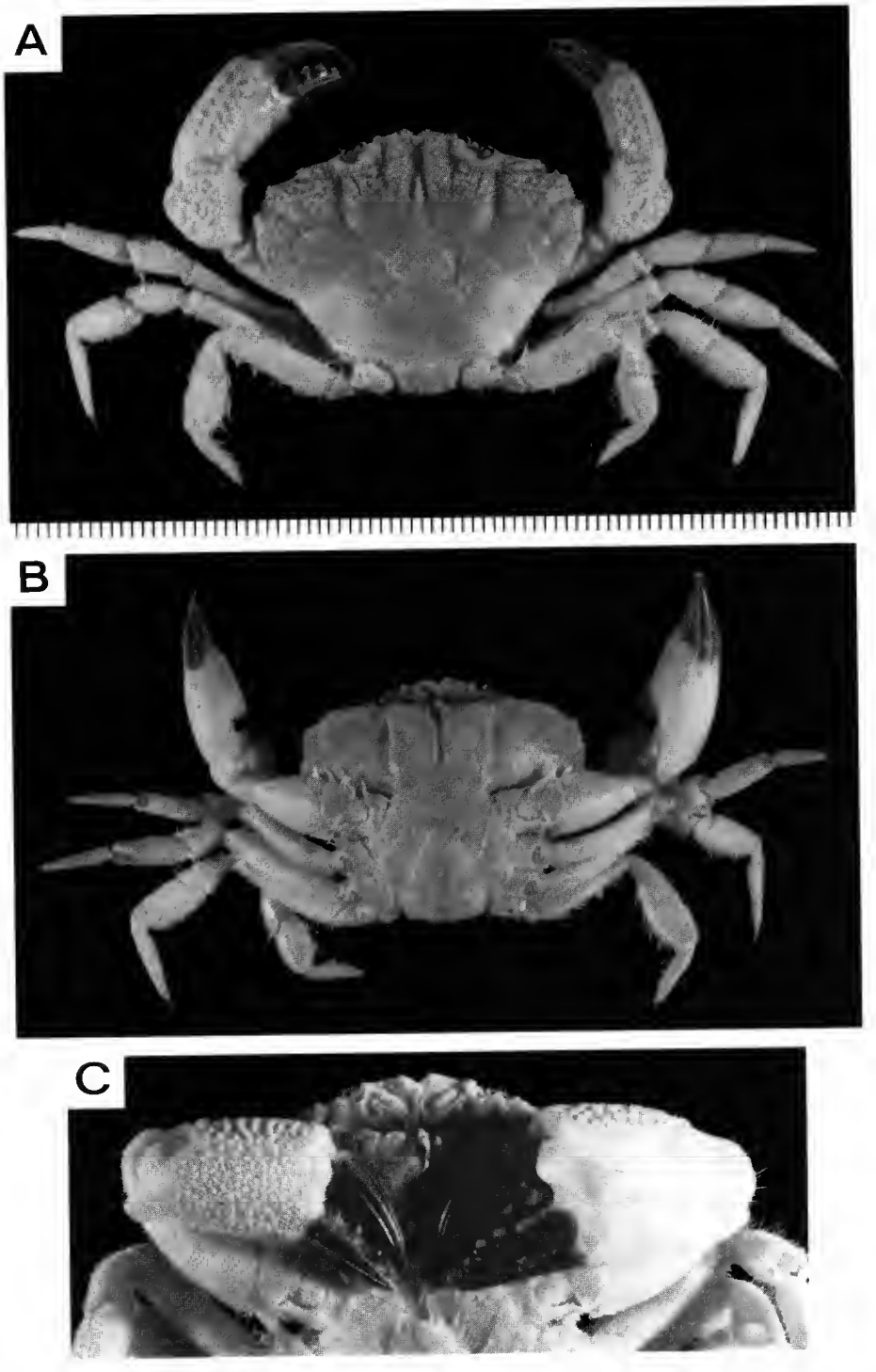

PLATE 7. — *Epistocavea mururoa* gen. nov., sp. nov. Paratype ♀, MNHN-B22234, Mururoa, Tuamotu Archipelago. A, dorsal view ; B, ventral view ; C, frontal view, showing chelipeds. Scale in mm.

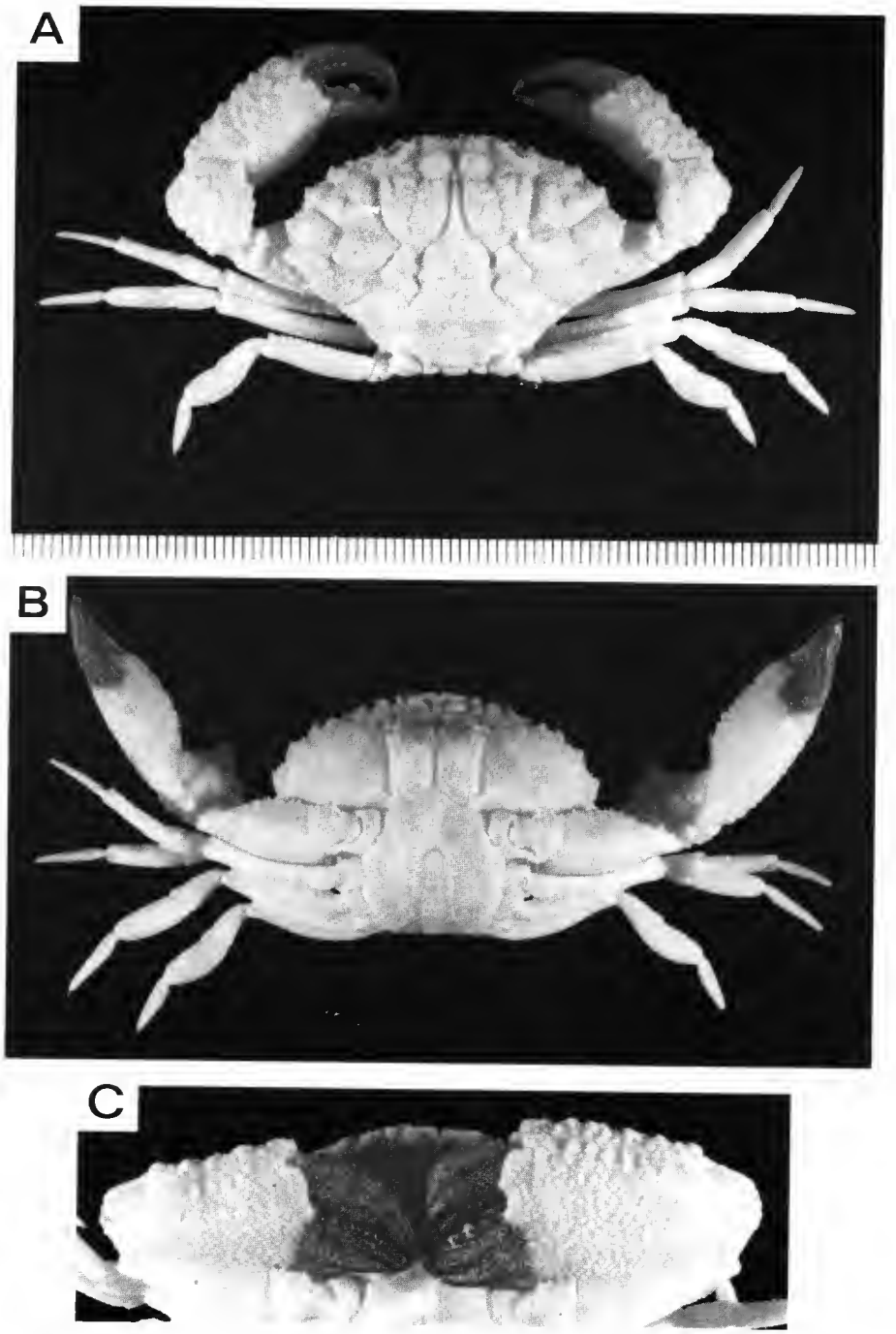

PLATE 8. — *Medaeus grandis* sp. nov. Holotype ♂, MNHN-B22218, Mururoa, Tuamotu Archipelago. A, dorsal view ; B, ventral view ; C, frontal view, showing chelipeds. Scale in mm.

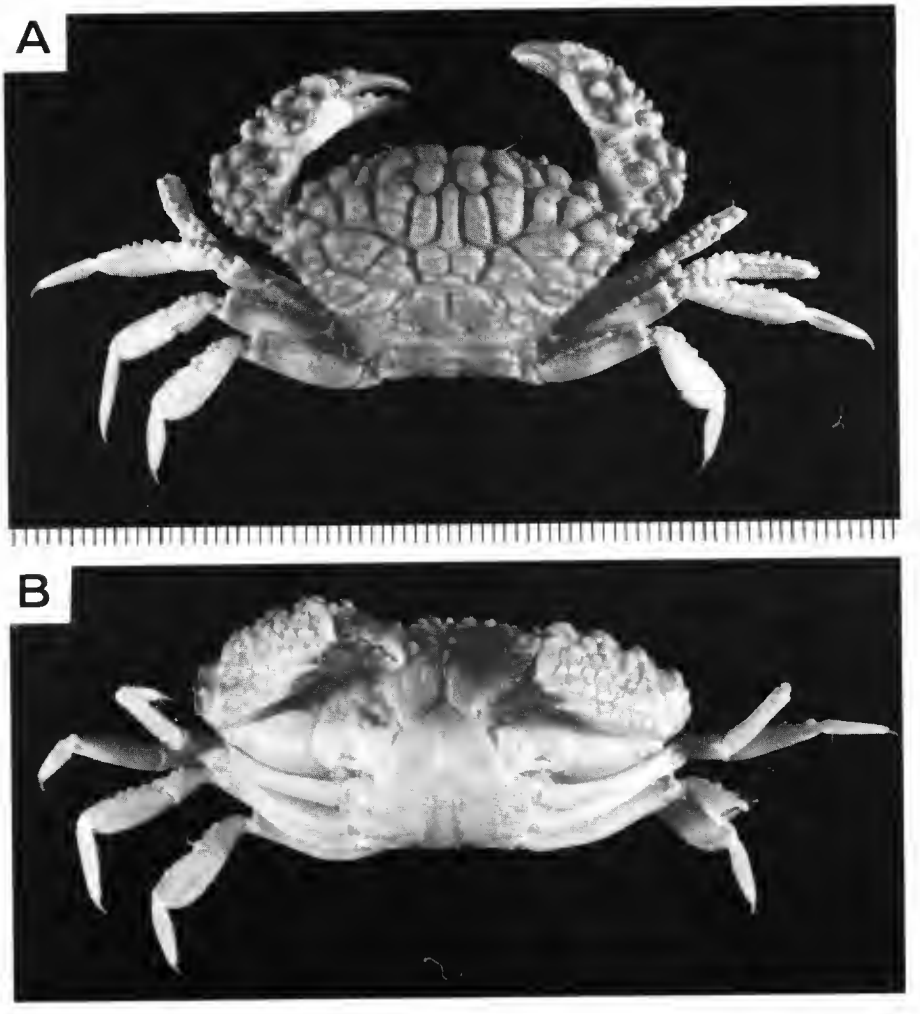

PLATE 9. — *Meractaea tafai* gen. nov., sp. nov. Holotype ♂, MNHN-B22216, Acteons Maria, Tuamotu Archipelago. A, dorsal view ; B, ventral view. A, dorsal view ; B, ventral view. Scale in mm.

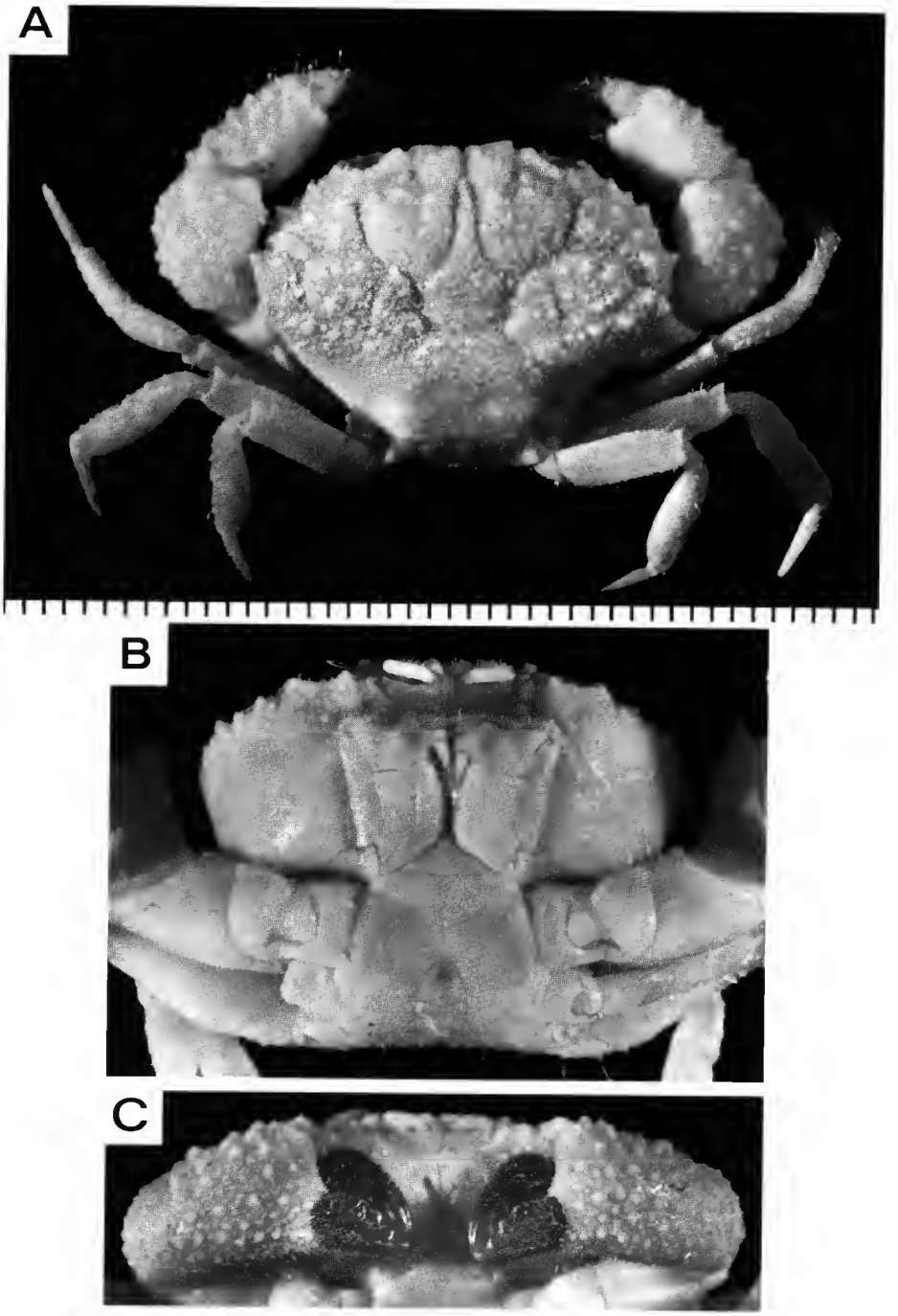

PLATE 10. — *Rata tuamotense* gen. nov., sp. nov. Holotype ♂, MNHN-B22231, Fangataufa, Tuamotu/Gambier Archipelago. A, dorsal view ; B, ventral view ; C, frontal view, showing chelipeds. Scale in mm.

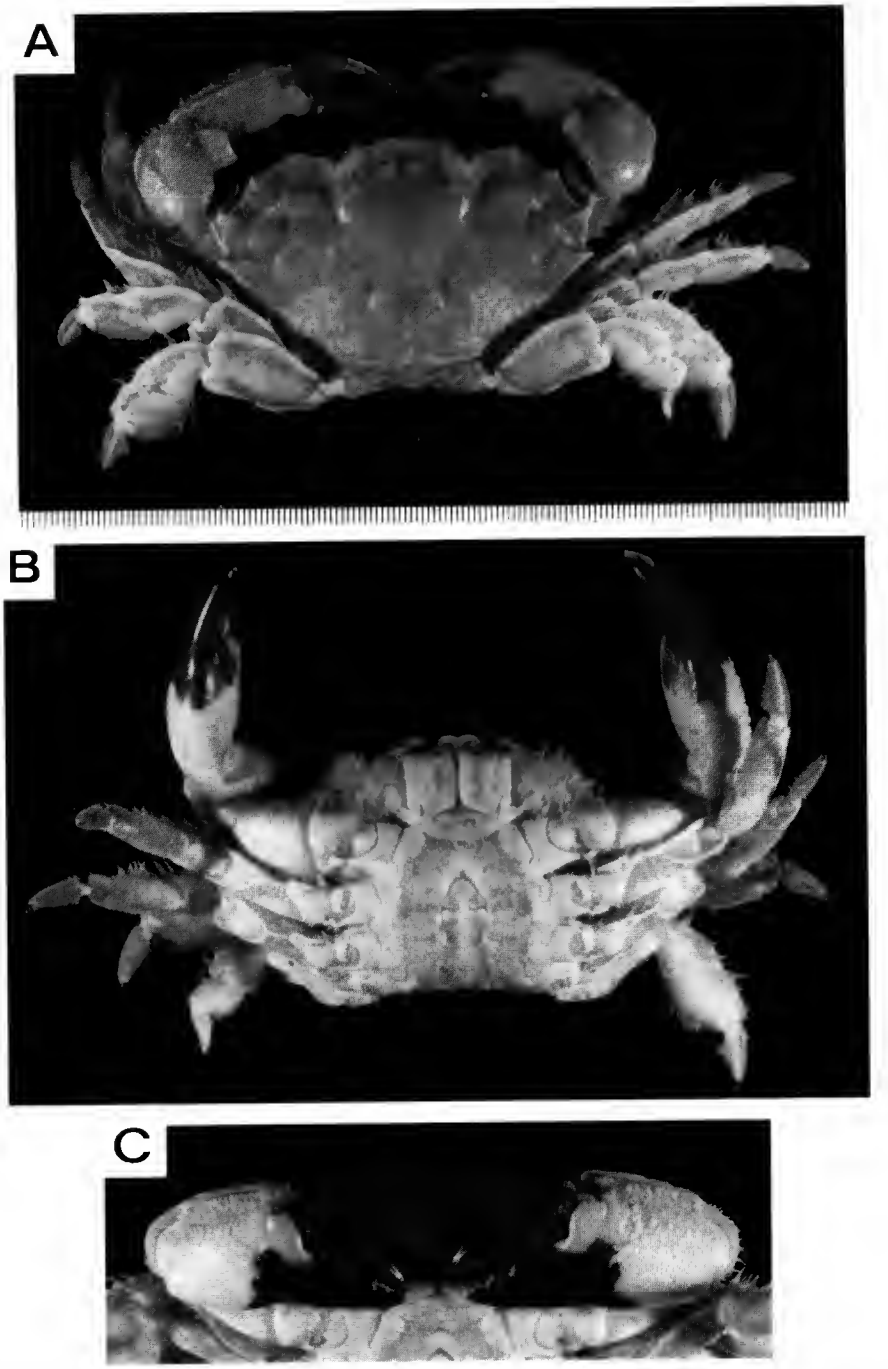

PLATE 11. — *Lophozozymus bertonciniae* Guinot and Richer de Forges, 1981. ♂, QM W8030, Hiva-Oa, Marquises Archipelago. A, dorsal view ; B, ventral view ; C, frontal view, showing chelipeds. Scale in mm.

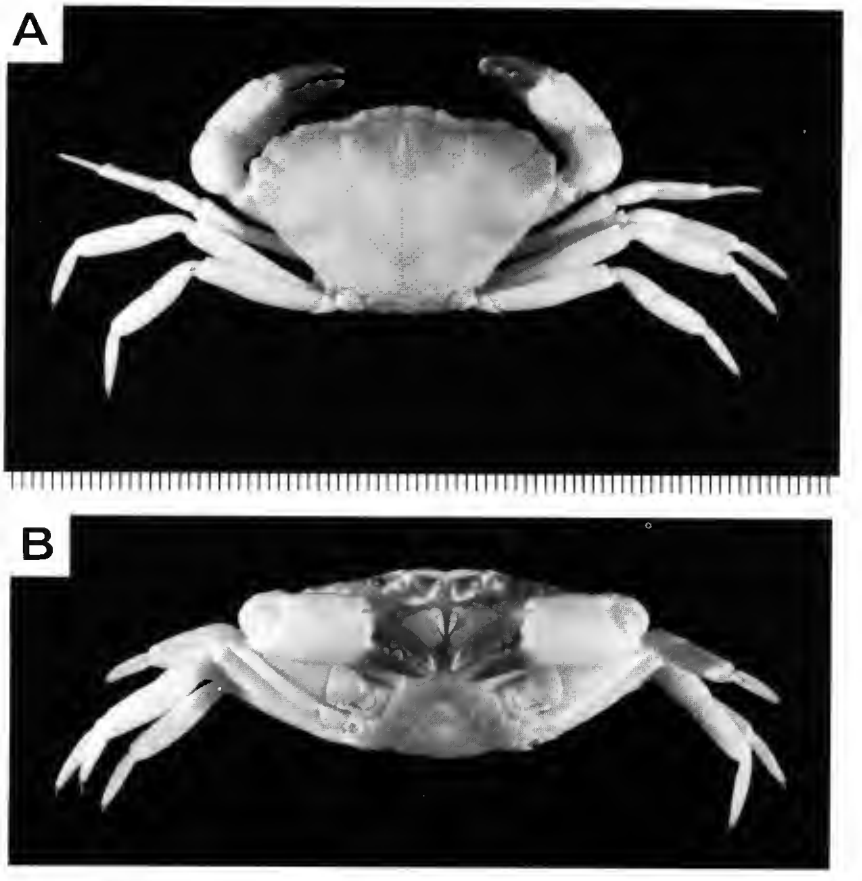

PLATE 12. — *Meriola rufomaculata* gen. nov., sp. nov. Paratype ♀, MNHN-B22222, Fangataufa, Tuamotu/Gambier Archipelago. A, dorsal view ; B, frontal view. Scale in mm.

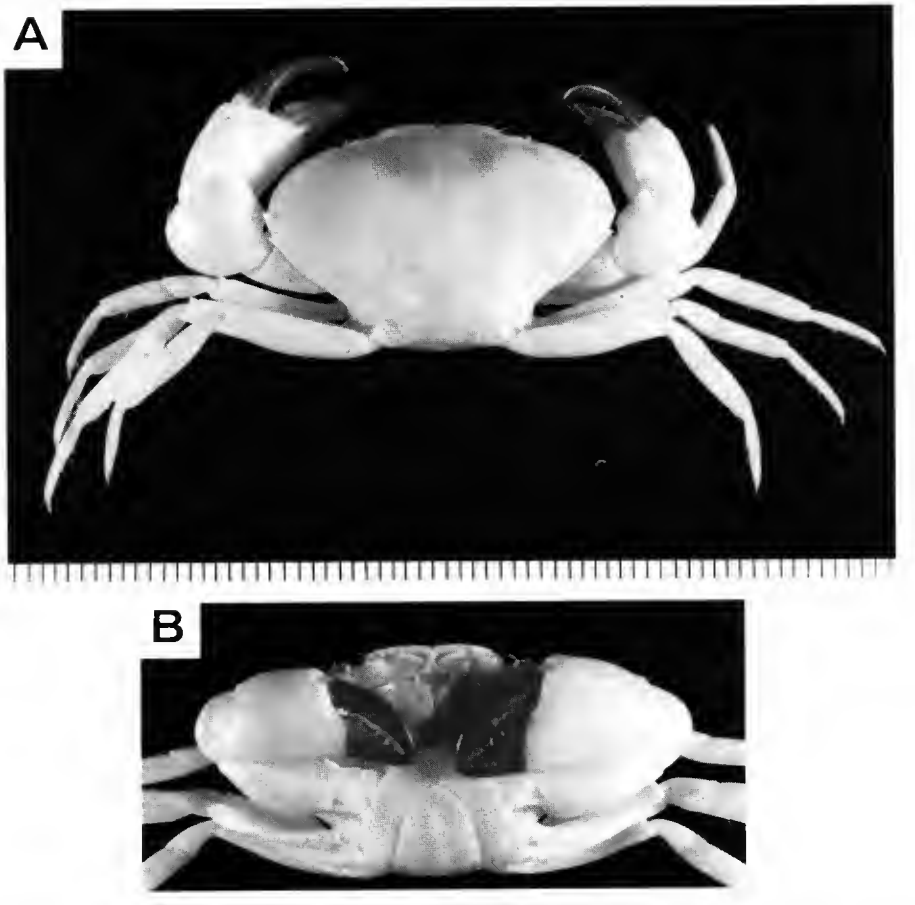

PLATE 13. — *Euryozius danielae* sp. nov. Holotype ♀, MNHN-B22217, Maupiti, Society Islands. A, dorsal view ; B, frontal view. Scale in mm.

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